Research Topics

Ecological nutrient management as a pathway to zero hunger

Edited by
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Steven J. Vanek

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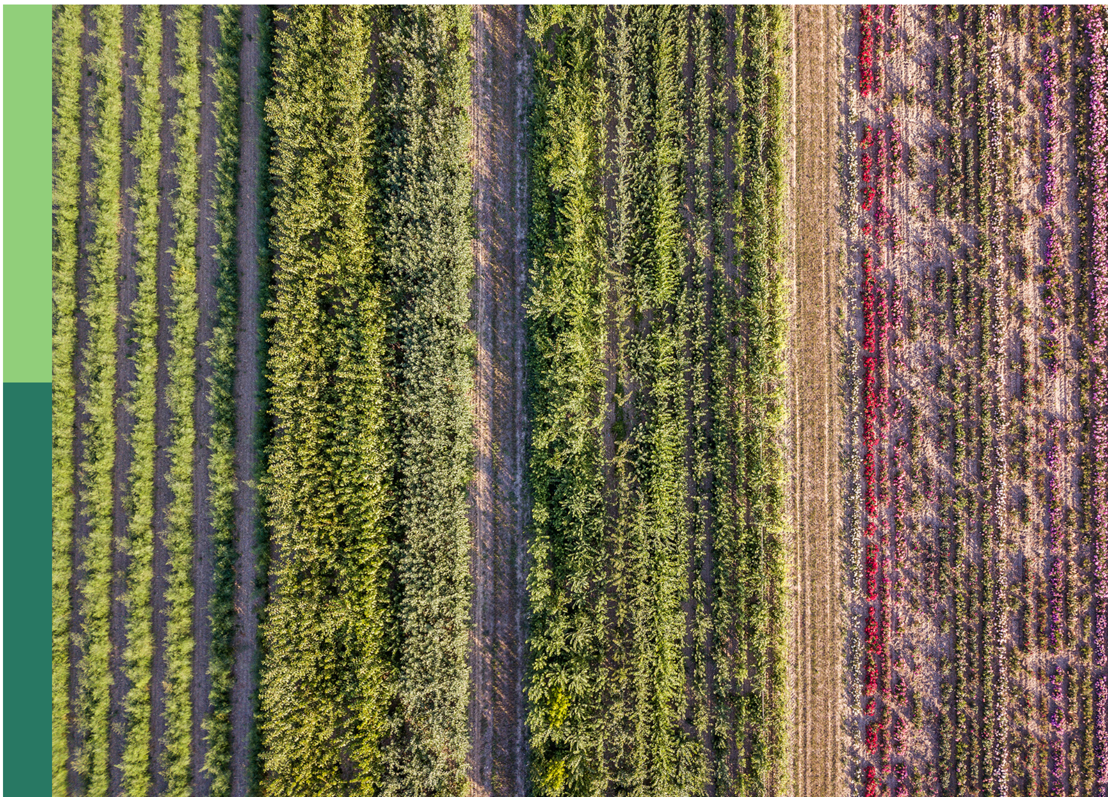

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Ecological nutrient management as a pathway to zero hunger

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Editorial: Ecological Nutrient Management as a pathway to Zero Hunger

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Editorial on the Research Topic
Ecological Nutrient Management as a pathway to Zero Hunger

The second United Nations Sustainable Development Goal (SDG 2, or *Zero Hunger*) integrates five ambitious targets for agricultural sustainability, social equity, and human health (Figure 1; UN, 2015). Embedded in these targets are key ecological processes in agroecosystems, such as water and carbon (C) storage, nutrient cycling, and pest regulation. By contributing to social and ecological system resilience, these processes help to safeguard the future production of nutritious food (Blesh et al., 2019). The SDG 2 targets also include conservation of cultivated and wild species of plants and animals, and equitable access to critical resources for agricultural production, such as land, credit, markets, and knowledge. This Research Topic provides key interdisciplinary examples of social-ecological systems approaches required to achieve SDG 2.

A recent confluence of shocks—COVID-19, climate change, and the Ukraine-Russia conflict—have deepened food insecurity and hunger, making SDG 2 an even more urgent humanitarian priority. Although these crises have motivated calls to strengthen an industrial approach to agriculture that deepens reliance on non-renewable resources (e.g., USDA, 2022), they have fortunately also invigorated proposals to expand resilient and sustainable agroecosystems that better fulfill the broad and interconnected targets of SDG 2 (e.g., McGreevy et al., 2022). For instance, rising input prices from spikes in the price of fertilizer made from natural gas are a main driver of rising food costs, and thus food insecurity.

Globally, nitrogen (N) and phosphorus (P) are the nutrients that most often limit crop yields, yet widespread use of soluble N and P fertilizers contributes to climate change *via* greenhouse gas emissions, and to water pollution, both of which, in turn, threaten future food production and human health. The simplification of production systems, and the continued singular reliance on synthetic fertilizer inputs for nutrient management, have disrupted nutrient recycling and depleted stocks of soil organic matter (SOM) on farms, and increased N and P losses to the environment. This soil degradation, in combination with crop varieties bred to require inorganic fertilizers, undermines the achievement of SDG 2. In this Research Topic, we focus on Ecological Nutrient Management (ENM) as a holistic approach to managing agroecosystems to sustain crop production while reducing dependence on synthetic inputs.

This Research Topic brings together 12 papers on ENM as a pathway to Zero Hunger to summarize the state of the science, highlight opportunities and barriers to the expansion of ENM, and identify research needs to support its expansion. To frame the collection, Drinkwater and Snapp introduce five key principles of ENM. Each principle connects—directly or indirectly—to the targets of SDG 2, demonstrating how ENM is a mechanism for realizing the multifunctional goals of SDG 2 that link agriculture, environment, and human health (Figure 1). By increasing agrobiodiversity and reducing the need for purchased inputs, ENM increases ecosystem health while advancing social equity through greater farmer autonomy. Crop and livestock diversity can also support access to diverse markets, buffer against risk, and improve the quality of diets through multiple pathways (Powell et al., 2015; Jones, 2017).

Build SOM and nutrient reserves

Drinkwater and Snapp review recent scientific advances in the understanding of SOM stabilization, and interactions in the

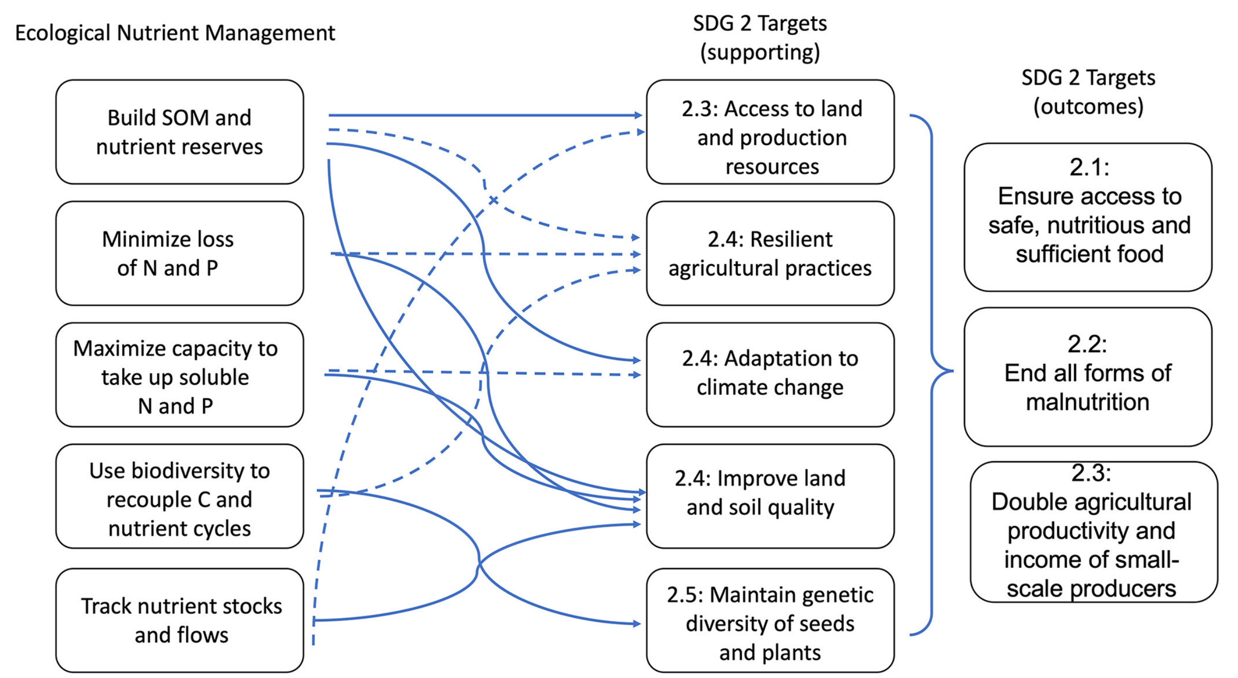

FIGURE 1
Conceptual diagram showing pathways that link Ecological Nutrient Management (ENM) to the 5 targets of the second Sustainable Development Goal (SDG 2, Zero Hunger). In their review, Drinkwater and Snapp introduce five key principles of ENM **(left side)**: (1) build soil organic matter (SOM) and associated nutrient reserves; (2) minimize the soluble pools of nitrogen (N) and phosphorus (P) that are vulnerable to loss; (3) maximize the capacity for agroecosystems to take up and cycle soluble nutrients; (4) increase biodiversity to maximize the presence of growing plants and recouple C, N, and P cycles; and (5) use mass balances to assess net nutrient stocks and flows over multiple growing seasons. We show the links between these principles and the five SDG 2 targets, which are organized into two columns, "supporting" and "outcomes." This distinguishes the components of the five targets that are intended to support high-level outcomes for SDG 2, shown at the far right of the diagram. Solid arrows show direct links between ENM principles and supporting targets of SDG 2, while dashed arrows show indirect links. These links include: ***Building SOM and nutrient reserves*** directly improves production resources and soil quality, and indirectly contributes to resilient systems by enhancing nutrient cycling and provisioning, reducing the need for external inputs, and buffering agroecosystems against drought and flooding. ***Minimizing losses of N and P*** directly improves land and soil quality by maintaining nutrient stocks in soils, and indirectly increases the resilience of agricultural practices by increasing the efficiency of nutrient inputs and reducing pollution of surrounding ecosystems. ***Maximizing agroecosystems' capacity to take up soluble N and P*** directly improves land and soil quality *via* nutrient storage and increased productivity, and indirectly supports climate change adaptation by reducing farmers' reliance on expensive, non-renewable inputs. ***Increasing species and functional diversity*** to recouple C with nutrient cycles directly maintains or increases crop diversity, and indirectly increases resilience by increasing productivity, buffering against market shocks, and increasing the capacity for adaptation to climate change. Using mass balances to ***track net nutrient stocks and flows*** directly improves land and soil quality by reducing nutrient surpluses and identifying deficits; it also indirectly increases farmer knowledge that improves management practices.

rhizosphere (i.e., the zone of soil closest to plant roots) that supply nutrients to crops, with a focus on ENM in smallholder systems in sub-Saharan Africa. Building SOM is also important for restoring soil quality in the Global North and can be realized most quickly by cultivating perennial species on farms. Mosier et al. and Martin and Sprunger discuss perennial cropping systems that could be adopted in the near term to restore degraded soils, while Crews et al. study a highly transformative perennial management system that involves intercropping a forage legume with a perennial cereal crop.

Maximize capacity to take up soluble N and P, and minimize nutrient losses

Several papers address mechanistic questions about ecological processes that store and cycle nutrients in agroecosystems, while exemplifying methods needed for robust understanding of ENM practices. Mosier et al. review mechanisms that stabilize soil C and retain N and P, while fostering the availability of these key nutrients. In an on-farm study in British Columbia, Norgaard et al. evaluate strategies to balance the stoichiometry of N and P in organic nutrient amendments to improve soil nutrient retention. Meanwhile, Martin and Sprunger move beyond traditional agronomic metrics of N availability in maize agroecosystems, such as extractable N and crop N uptake, to instead focus on plant-soil-microbial interactions (the microbial loop) that regulate organic N cycling. Finally, Isaac et al. review literature and global trait databases to assess the effects of crop domestication on root functional traits, and discuss implications for crop nutrient acquisition within the context of ENM. They emphasize the need for new crop breeding paradigms to support SDG 2, particularly Target 2.5 to maintain genetic diversity of domesticated crops (Figure 1).

Moving beyond the field and farm scale, two papers in this collection focus on recovering nutrients from urban areas and returning them to rural areas to improve soil fertility for crop production. The paper by Ryals et al. examines a number of potential ENM impacts (crop production, soil nutrient cycling and losses) of closed loop sanitation systems (EcoSan) with implications for regional circular nutrient economies. These systems couple household toilets with composting to recycle nutrients to food production. Harder et al.'s innovative proposal for regional scale modeling assesses food system scenarios that facilitate circular nutrient flows. The authors account for flows in interacting systems and sectors outside the region boundary, improving analyses that can inform how to reduce waste and use of external inputs on farms.

Track net nutrient stocks and flows

The application of nutrient mass balances in research and practice is another core principle of ENM that could help achieve the targets of SDG 2, such as improving the quality of soil and surrounding ecosystems by reducing nutrient surpluses and increasing farmer access to knowledge to improve the sustainability of nutrient management practices. Crews et al. demonstrate the value of collecting detailed N-flux measurements over a 5-year period to inform sustainable N management. Witcombe and Tiemann apply partial N balances to working farms to understand how farmers' management decisions affect the trajectory of soil fertility.

Use biodiversity to recouple C and nutrient cycles

The studies on perennial cropping systems, together with Perrone et al.'s experiment on overwintering cover crops, reinforce that legumes and perennials are essential plant functional groups for restoring soil fertility and building SOM, impacting multiple outcomes depending on their specific functional traits and how they are managed by farmers. These studies thus inform how to manage agrobiodiversity to recouple C and nutrient cycles. For instance, perennial legumes—whether harvested or not—can build soil C and N pools and enhance internal nutrient cycling and availability to crops (Crews et al.; Mosier et al.). Annual legumes, on the other hand, may not have a detectable effect on soil C and N pools if harvested (Witcomb and Tiemann), but they provide a healthy source of protein for human diets. In contrast, non-harvested legume cover crops are not consumed by people but can build multiple SOM pools (Drinkwater and Snapp) and increase soil N availability, even in cold northern climates that limit cover crop biomass production (Perrone et al.).

Zimmerer et al.'s study identifies multifunctional outcomes of crop diversification in Peru. The authors analyze social, political, and ecological factors influencing agrobiodiversity on smallholder farms and gardens, and their associated impacts on ENM. The authors define the concept of a "key agrobiodiversity-and-food space" as a management system with a high likelihood of having multiple positive outcomes related to SDG 2, particularly the targets for maintaining genetic diversity and improving human nutrition. In their study site, *Maizales*, or fields that combine maize with other crop species, are a "keystone" management system linked to enhanced agrobiodiversity, ENM practices, and food and market opportunities for smallholder farmers.

Barriers to implementation of ENM

Several papers in the collection discuss the multi-level, social-ecological constraints to ENM. Nyamasoka-Magonziwa et al. conduct focus groups and survey 184 farm households in East Africa to understand economic, cultural, and environmental drivers of organic nutrient management. Their results highlight the importance of access to resources, gender dynamics, and land tenure in driving farm management decisions. Drinkwater and Snapp, Mosier et al. and Isaac et al. summarize key challenges to adoption of ENM on farms, such as a lack of financial incentives and markets for diversified cropping systems; policies that emphasize short-term productivity over long-term ecosystem resilience; the need for seeds bred for organic systems; and the need for greater dissemination of agroecological knowledge. These multi-scale barriers point to the need for democratic policies that conserve nature, provide fair prices for farmers, and ensure that all people have access to nutritious food.

Future directions for research and the SDGs: Taking ENM seriously

The papers in this collection highlight research needs that can help overcome barriers to implementation; specifically, supporting research on micro-scale mechanisms, embracing complexity in on-farm research, and designing cross-scale studies to close nutrient loops. Ecological mechanisms at the micro-scale that conserve C and nutrients in soil (e.g., interactions between plant roots, microbial communities, and soil mineralogy) are a complex scientific frontier of ENM that can build generalizable knowledge to adapt to local contexts. This line of inquiry could be extended to understand connections between soil nutrient management, crop nutrient status, and human nutrition. There is also a need for participatory, on-farm research to better understand the myriad factors that influence farmers' transitions to ENM. Such studies could zoom in on positive models of innovation to understand processes that facilitate ENM, and the associated benefits for the SDG 2 targets. Or, this work could identify how to phase out unsustainable forms of nutrient management (Geels et al., 2017). This collection also highlights the need for interdisciplinary, cross-scale studies to scale up innovative technologies such as perennial crops, which have promise for building SOM, conserving soil nutrients, and minimizing nutrient losses (Zhang et al., 2022). Additionally, new technologies and infrastructure for waste capture and recycling are needed to close loops between urban and rural spaces and reduce nutrient losses to the environment at landscape and regional scales.

The UN's Agenda for Sustainable Development resolves to achieve Zero Hunger by 2030, which is on the horizon. Continuing to incentivize an industrialized approach to agricultural nutrient management has not put us on a trajectory to achieving this goal and continues to exacerbate environmental and human health crises. This leads us to ask: when will we embrace the experiential and scientific evidence pointing to ENM as a pathway to ending hunger?

Author contributions

JB suggested the Research Topic and wrote the initial draft of this editorial. All authors contributed to conceptualization, writing and editing, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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ORIGINAL RESEARCH
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Organic Nutrient Source Allocation and Use in Smallholder Farming Communities: What Are We Missing?

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Organic nutrient sources (ONS) are managed as a key resource by smallholder farmers to maintain the productivity of soils. Recycling of ONS by applying them to soils is a globally dominant strategy of ecological nutrient management. Understanding how ONS produced on-farm are allocated and what drives farmer decision making around their use is critical for sustainable nutrient management in smallholder agroecosystems. Using focus group discussions and a survey of 184 farming households, we studied socio-economic, socio-cultural, and environmental drivers of ONS allocation and use at the farm scale in three contrasting agroecological zones of western Kenya. Farm typologies of ONS management were also developed using cluster analysis based on resource endowment and the connectedness of farmers, management norms, and interaction with extension. Our findings suggest that the more resource endowed a farmer is, the more ONS are allocated to the main plot within the farm. We also observed that farmers preferred allocating more resources to plots that were considered more fertile. Land tenure had an important influence, in that main plots not owned by farmers were more likely to retain ONS such as crop residues. Management of residues is dependent on farmer gender, for instance, female farmers tended to burn legume residues in particular, which is notable since these higher quality residues are often considered key to sustainable soil nutrient management. Farm typologies featured different allocation patterns of ONS and were associated with resource endowment and farmer networks, including external ties to extension agents and internal ties to other farmers. Finally, there was a strong overarching influence of agroecological zone that often escapes characterization on the allocation of ONS. As research and development organizations continue to engage with smallholder farmers to reduce the burden of global food insecurity, the insights gained by this research will allow better anticipation of drivers and obstacles to improved nutrient management in these farming landscapes and communities.

Keywords: soil health, cereal-legume-livestock systems, crop residues, manure, socio-cultural, ecological nutrient management

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INTRODUCTION

On many smallholder farms around the world, crop yields remain low (i.e., around 1 Mg ha^{-1} for staple cereals; Tittonell and Giller, 2013) or are declining due to inherently poor soils and inadequate soil fertility management, among other factors (Sheahan and Barrett, 2017; Khalid et al., 2019). Poor soil health thus threatens the achievement of Sustainable Development Goal Two (SDG2), which aims to end hunger, achieve food and nutritional security, and promote sustainable agriculture. Recycling organic nutrient sources (ONS) produced on farm by applying them to soils, with or without mineral fertilizer additions, can increase soil organic matter (SOM) and nutrient cycling, and hence improve soil health (Agegnehu and Amede, 2017). The role of organic amendments in sustainable agriculture is highly relevant, and understanding how they are managed and implications for soil fertility in different farming systems and contexts can contribute to meeting these SGD2 targets.

Smallholder farmers produce and manage organic resources such as crop residues (Valbuena et al., 2012; Turmel et al., 2015), animal manure (Rufino et al., 2007) and farmyard manure/compost on farm. They may also collect off-farm organic resources, such as forest litter or plant residues from field margins, to apply in their soils as a key source of nutrients for their crops (Nekesa et al., 2007; Nganga et al., 2020). Different types of organic inputs play distinct roles in the improvement of soil health by increasing SOM and in providing nutrients to support crop productivity (Rusinamhodzi et al., 2016; Wood et al., 2018; Vanlauwe et al., 2019). Studies in western Kenya have demonstrated the potential that ONS have to improve nutrient use efficiencies and ultimately crop yields, especially when combined with mineral fertilizers (Vanlauwe et al., 2011; Mutuku et al., 2020). Studies by Lu (2020) and Murphy et al. (2016) demonstrate that residue retention led to increased crop yields, soil organic matter content and nutrient use efficiency e.g., the latter found that residue retention led to roughly twice as much fertilizer nitrogen making it into maize plants and a 40% increase in overall "system" recovery (plant + soil). A range of ONS have long been used by farmers in their cropping fields and home gardens, sometimes in combination with mineral fertilizers (Palm et al., 1997). More recently, soil management approaches such as conservation agriculture and integrated soil fertility management further promote the use of ONS to manage soil fertility and overall health. Practices involving ONS have been shown to minimize losses through leaching and erosion and improve nutrient use efficiency (Agegnehu and Amede, 2017).

Farmers are often faced with decisions on how to allocate ONS around the farm. Some may retain all the residues produced in the plot where they grew, applying them directly to the soil, whilst others may transfer them to other plots (Rusinamhodzi et al., 2016). Farmers with livestock may choose to feed some or all of the residues to livestock and then apply the manure produced directly (or composted) as an ONS (Rufino et al., 2007). Some ONS can also be used as fuel and building materials, thus highlighting numerous potential tradeoffs for ONS allocation, with important implications for nutrient management and soil health. For example, if maize residues are exported from a plot season after season, without other inputs coming in, severe nutrient and SOM depletion will occur resulting in poor crop yields. Several studies have assessed the general management of crop residues and manure at the farm level in East Africa and particularly in western Kenya (e.g., Tittonell et al., 2005; Valbuena et al., 2012; Rodriguez et al., 2017). These studies have focused largely on the issue of organic input allocation and associated tradeoffs and pose the question of which is the best way to allocate organic resources to benefit soil health, livestock production and/or off farm trade.

Meanwhile, other studies have focused on practices in the use of ONS and have considered determinants of adoption of ONS, largely focusing on the resource status of farmers (Pedzisa et al., 2015; Adolwa et al., 2019). Economic resource endowment of farmer households has been shown to be a key driver of nutrient management practices, specifically the use of ONS in smallholder farms because it influences the quantity of organic resources available (Mugwe et al., 2009; Liu et al., 2018). For example, the more livestock a farmer has, the more manure they can put in their field, but the less crop residues they may retain in-field due to need for feed (Duncan et al., 2016). More resource endowed farmers might also allocate less ONS to the field since they can afford to purchase mineral fertilizers. However, beyond farm resource endowment, there are other socio-economic factors such as land tenure, access to local extension and training. A clearer understanding of socio-cultural variables such as adherence to social norms and social networks that influence ONS allocation is needed (Mponela et al., 2016; Leonhardt et al., 2019). These additional factors remain poorly understood and thus may be obscuring constraints and opportunities for more effective and accessible ecological nutrient management within smallholder farming systems. A clearer understanding is required of socio-cultural variables that could influence decisions on how organic resources are allocated around the farm. Such understanding can help to foster socio-ecological based approaches that are required to understand the adaptive capacity (i.e., ability to cope with environmental and societal changes) of agricultural systems (Folke et al., 2002). This adaptive capacity is especially important for soil nutrient management to achieve zero hunger by the most vulnerable farming communities in smallholder farming systems.

In addition to socio-cultural factors at a household scale, it is important to recognize that environmental factors (agroecological zone and within-farm soil variability influenced by preferential allocation of ONS to some plots) affect ONS management in smallholder systems. Communities vary in terms of land holding, farming systems, organization and social norms when comparing different agroecological regions (Tittonell et al., 2005). Meanwhile, at the farm scale, soil fertility gradients are created due to preferential allocation of ONS in different plots, and this creates feedbacks that cause fertile soils to improve and infertile soils to become more depleted creating within-farm variability (Vanlauwe et al., 2007; Zingore et al., 2007; Masvaya et al., 2010). The perception of plot fertility resulting from the gradients and distance from homestead which influences labor available also determine where farmers allocate their ONS (Caulfield et al., 2020).

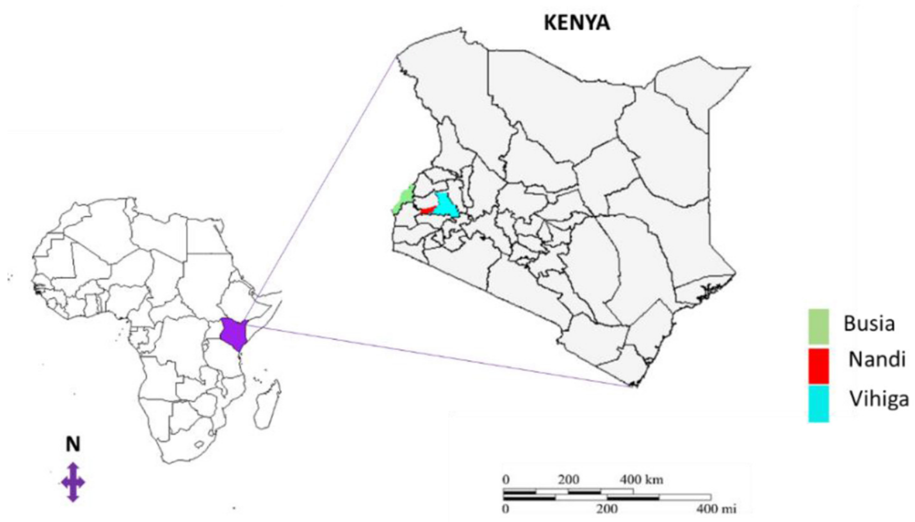

FIGURE 1 | The study sites Busia, Nandi, and Vihiga counties in western Kenya.

Given the interplay of social and environmental factors at different scales, smallholder farmers occupy very specific niches embodying socio-economic and socio-cultural factors as well as agroecological contexts and variability that they themselves may create on their farms (Ojiem et al., 2006). As such, it is helpful to group farmers/farms that are similar (*via* typologies or other means) to better understand their utilization of soil fertility practices and/or to generally characterize farmers (Alvarez et al., 2018). While resource endowment is clearly important in developing such farmer typologies (Tittonell et al., 2005; Chikowo et al., 2014), socio-cultural variables may also influence ONS management (Tittonell et al., 2005; Kolawole, 2013) and it is important to understand how and to what extent such variables also influence the formation and characterization of ONS management. It is also important to link environmental and socio-economic approaches for different contexts in addressing issues of food security and soil quality (e.g., Webb et al., 2013; Kristjanson et al., 2017; Balch et al., 2020). Research in this area can benefit greatly from employing both quantitative and qualitative approaches to understanding the complex patterns of socio-economic status and agricultural development.

This study sought to improve our understanding of how the socio-economic, socio-cultural and environmental contexts influence decisions on ONS management in representative smallholder farms of western Kenya, so as to inform strategies for achieving sustainable soil nutrient management for "zero hunger" in vulnerable communities. Specifically, we wanted to understand: (i) how ONS are allocated and cycled at farm and community levels in contrasting agroecological regions, and (ii) the dominant socio-economic and socio-cultural factors affecting ONS allocation and cycling for different farm types, within a farm typology based on resource endowment, adherence to social norms, and connectedness to networks regarding soil management. We hypothesize that resource endowment together with key socio-cultural variables (e.g., gender, network connections, adherence to social norms, extension, training) and biophysical aspects, such as differences in agroecological contexts (location—which influences climate, soils, and farming systems and perceived soil fertility), are also significant determinants of ONS management. In summary, we hypothesize that these different determinants are expressed as farm types that help to explain different ONS management strategies in the mixed crop-livestock systems of western Kenya.

To address these questions, we conducted focus group discussions followed by quantitative farmer interviews in a mixed methods research approach carried out in three communities within contrasting agroecological zones in western Kenya.

METHODOLOGICAL APPROACH

Study Sites

The study was carried out in western Kenya in the counties of Nandi, Busia, and Vihiga (**Figure 1**). Located in different agroecological zones, the three counties experience distinct climates (**Table 1**) and have unique farming systems.

These counties also have different biophysical characteristics; for example, the soils in Nandi are typically ferralsols and acrisols, Vihiga is dominated by nitisols, while soils in Busia are typically acrisols (Agriculture Organization for the United Nations, 1998). Although the soils differ in terms of SOM content and iron and aluminum oxide concentrations, they generally have similar challenges of poor soil fertility associated with declining SOM, low base saturation, low cation exchange capacity, high phosphorus fixation and high soil acidity (Sanchez, 2019). Major types of agricultural production in these counties include smallholders with subsistence and some cash crops

TABLE 1 | Climate and location data for three counties in western Kenya where farmers were surveyed to evaluate allocation of organic nutrient sources in smallholder farming communities.

County	Location (coordinates)	Altitude (m.a.s.l.)	Average temperature (° C)	Average annual precipitation (mm)	Köppen-Geiger climate type*
Busia	0° 26′ 0″ N, 34° 9′ 0″ E	1,165	22.4	1,239	Aw and Am-tropical savanna
Nandi	0° 10′ 0″ N, 35° 9′ 0″ E	1,984	17.4	1,551	Cfa-Humid subtropical and Af-tropical rainforest
Vihiga	0° 4′ 0″ N, 34° 40′ 0″ E	1,643	20.0	1,921	Af-tropical rainforest

*Köppen-Geiger Rohli et al. (2015).

TABLE 2 | Nutrient content of selected organic inputs commonly produced and used on farm for crop production in western Kenya.

Organic Input		*N*	*P*	*K*	*Source*
			%		
Crop residues	Maize residues (*Zea mays*)	0.89	0.08	2.78	Okalebo et al., 2002
	common bean residues (*Phaseolus vulgaris*)	1.2	0.13	2.06	
	Napier grass (*Pennisetum purpureum)*	1.02	0.11	2.63	
	Lablab *(Lablab purpureus*) prunnings	1.31	0.33	-	
Manures	Cattle manure fresh/composted	1.12	0.3	2.38	Lekasi et al., 2003
	Poultry manure	3.11	0.42	2.40	Okalebo et al., 2002
	Farmyard manure	1.81	0.3	0.9	*unpublished data*
	Compost	1.34	0.20	1.82	Okalebo et al., 2002
Others	Biochar	0.56	0.03	0.73	*unpublished data*
	Tithonia diversifolia prunings	3.5	0.37	4.1	Jama et al., 2000

(average < 1 ha land holding), mainly of maize (*Zea mays L.*) intercropped with common bean (*Phaseolus vulgaris*); crop-livestock production (dairy, beef, small ruminants and poultry); cash crop production (mainly tea, *Camellia sinensis)* in Nandi and Vihiga and sugarcane (*Sacharum officinarum*) in Busia (Tittonell et al., 2009; Sorre, 2017; Oduor et al., 2019). The integration of field crops, forage crops such as napier grass (*Pennisetum purpureum)* and horticultural crops such as vegetables and fruits are also common feature of these farms. The farms therefore produce a variety of organic resources from the crops grown and animals reared on farm, which have potential to return major nutrients (nitrogen, phosphorus, and potassium) in varying quantities to the fields (see **Table 2**).

Study Approach

Data collection involved two main two activities: (i) qualitative focus group discussions, and (ii) a structured household survey.

Focus Group Discussions

Three focus group discussions were conducted in western Kenya, one in each county in July 2018 to understand the general ONS management practices in each community. Each focus group comprised a mixed group of 11 or 12 farmers, divided roughly equally by gender and a mix of age groups, but dominated by farmers more than 30 years old (∼80%). A facilitator fluent in the local languages and familiar with agricultural practices in the region helped to facilitate the discussions. Notes were taken in local languages and later translated to English. The discussions (∼2 h each) were guided by the following themes: Crop and livestock production, soil fertility, organic residue management and trade-offs among ONS uses, and connections of farmers to sources of information on soil fertility management.

Household Surveys

In June of 2019 a structured and pre-coded survey was administered in local languages to smallholder farmers in the three communities mentioned above (following approval by the Colorado State University Institutional Review Board) to understand the drivers of management and allocation of ONS (see **Table 4** and survey instrument in **Supplementary Material**).

About a third of farmers were sub-sampled from records of the Kenya Agricultural Livestock Research Organization (KALRO-Kibos) and two partner organizations working in the region (Appropriate Rural Development Agriculture Program and Avene Community Development Organization) using a stratified random sampling approach, where the farmers were stratified by gender of the household head. Each selected farmer also served as recruiter of two other farmers that were not involved in any project activities to reduce the bias from project involvement. Verbal consent was obtained from all farmers prior to beginning an interview (see **Supplementary Material**). The total number of farmer interviews was 184 (Nandi = 62, Busia = 60, and Vihiga = 62) and the sample was ecologically and socioeconomically representative of the county zones. The surveys were collected on touchscreen tablets using an open data-kit survey on the KoBo Toolbox platform (Harvard Humanitarian Initiative, 2018) by four trained enumerators.

The survey addressed *predictor* variables for ONS allocation such as resource endowment, family demographics, and perceived soil fertility status and agroecological zone drivers (**Table 4**). In addition, information was collected on main residue types and quantities, as well as socio-cultural aspects related to contact with extension agents and local management norms. Meanwhile, survey *response* variables related to ONS and their role in nutrient management included the proportion of crop residues retained in the main plot and the proportion of cattle manure and poultry applied directly to the main plot (in composted and/or uncomposted forms—which gives insights on management of manure). Allocation to the main plot was taken as a key indicator of nutrient management with ONS since all farms had at least one main production field while not all had additional fields and previous studies have shown that ONS are applied preferentially to the main plot which makes it a benchmark for ONS management.

During the survey, a participatory modified 10-seed method (Jayakaran, 2002) was used to estimate the proportion of ONS allocated for different uses in relation to the total available. Farmers were given 10 beads representing the total ONS from a field or manure produced in that season. They were then asked to "allocate" the proportion of ONS they retained in-field, took to other fields or fed to livestock. This technique reduces recall bias over asking farmers to estimate actual amounts (Sawada et al., 2019; Wollburg et al., 2020).

Study Population Characteristics

The study population consisted of 75% of male headed households, but most of the respondents (54%) were women, i.e., the spouse of the household head (**Table 3**). Most of the household heads were moderately to well-educated (46% with some primary education and 47% with secondary education or beyond), while 7% reported no formal education. The households were generally large, with 69% having at least 5 people. Roughly 55% of the households reported being food secure for at least 8 months. Most households had at least two sources of income, but farming was the main livelihood for all households surveyed. Trade and business (34% or respondents) and remittances (34% of respondents) were mentioned as additional sources of income. Only 29% of the households had a formally employed household head (i.e., with an off-farm job).

Estimation of ONS Produced on Farm

Average total organic inputs were estimated for maize crop yields from farmer reported maize yield (Mg ha^{-1}) assuming a harvest index of 0.44 (Dawadi and Sah, 2012). Cattle and poultry manure produced in the main season (Long rainy season March to May) was estimated using the formula:

$$TM = ME{*}days{*}No.animals{*}(1 - m)$$

where TM is the gross total cattle and poultry manure (kg DM season^{-1}) produced, and estimated without removing possible losses in storage, feeding and respiration, ME is the amount of manure excreted by each animal [i.e., cattle = ∼20 kg day^{-1} animal^{-1} (Nennich et al., 2005)] and poultry = ∼0.13 kg day^{-1} animal^{-1} (Wiliams et al., 1999), days is the estimated length of the rainy season in days (i.e., 120 days), No. of cattle is the number of cattle or poultry a farmer has, and m is the estimated moisture content of the manures.

Data Handling and Statistical Analysis

The data were downloaded from KoBo Toolbox, cleaned, and standardized as needed. For example, livestock ownership was converted to Tropical Livestock units (TLU) by multiplying the number of livestock owned by a factor (cattle = 0.7, shee*p* = 0.1, goats = 0.1 and poultry = 0.01) according to Chilonda and Otte (2006). Adherence to social norms of crop residue management was determined by comparing responses of what the farmer does against what they think is normally done with residues or manures in their area.

All data analysis was done in R v 3.6.2 (R Core Team, 2019), where the variables used as predictors (**Table 4**) in all the models were selected using a PCAmix algorithm for mixed data sets which combines a principal component analysis (PCA) for continuous variables and multiple correspondence analysis for categorical variables in ClustofVar package (Chavent et al., 2014) to reduce redundant and highly correlated variables. As such, variables with squared loadings of < 0.3 were dropped from the analysis as suggested by Hair et al. (1998). Location and gender were retained as they have been shown to be important predictors in similar studies (e.g., Kristjanson et al., 2017; Liu et al., 2018). Factors explaining variability in the proportion of crop residues retained in-field and manure used (cattle and poultry) were determined using stepwise regression based on Akaike Information criteria (AIC) with the selected model having the smallest AIC value (Akaike, 1987). Data was tested for regression assumptions of normality, homogeneity of variance, linearity and independence. Differences in ONS inputs applied in the main plot and secondary field were determined using *t*-tests. A stepwise multinomial logistic regression model was used to determine factors important in explaining variability in the main use of crop residues using the package mlogit (Croissant, 2020). The model was tested for multicollinearity using the generalized variance inflation factor (GVIF) which was <2 (Fox and Monette, 1992) as well as other regression assumptions. Differences in ONS management between locations and characteristics were determined using ANOVA and fisher's exact tests. Tukey honestly significant difference (HSD) at $p < 0.05$ was used for pairwise comparisons between groups.

Development of Farmer Typologies for ONS Management

Types for ONS management were developed using hypothesis-based typology formation (Alvarez et al., 2018), where variables selected depend on the objectives of classification. The variables that were considered important in explaining variability in ONS management as selected by PCAmix and subsequently stepwise

TABLE 3 | Household demographic information and farm characteristics of smallholder farmers interviewed in Nandi, Busia, and Vihiga counties in western Kenya in June 2019.

Location	**Busia** **(n = 60)**	**Nandi** **(n = 62)**	**Vihiga** **(n = 62)**
	Number of households per category		
Gender of household head			
Female	13	19	15
Male	47	43	48
Household size (no. of members)			
2 or less	2	1	1
2–5	12	15	18
5–9	35	33	40
>10	11	13	4
Food sufficiency (months)*			
12	16	10	13
8–11	26	18	18
5–7	9	8	15
<5	9	26	17
Livelihood strategies			
Farming	60	60	62
Formal employment (off farm)	9	6	11
Trade and craft	15	21	27
Aid (government or NGO)	2	1	0
Others e.g., rentals	3	4	1
Education of household head			
No formal education	7	3	4
Primary education	26	31	27
Secondary (up to high school)	20	22	29
Tertiary and beyond	7	6	3
Mineral fertilizer use			
No	10	7	6
Yes	50	55	56
Tenure of main plot			
Owned	49	55	49
Rented/shared	11	7	13
Farm characteristics - Mean (SE)			
Livestock ownership (TLU)‡	2.48 (0.3)	1.64 (0.2)	1.51 (0.2)
Area of main plot (ha)	0.52 (0.07)	0.56 (0.07)	0.30 (0.03)

**Farmers where asked how many months in a year that they felt they had enough food to feed their household comfortably with 3 meals a day.*

‡Livestock ownership was converted to Tropical Livestock Units (TLU) by multiplying the number of livestock owned by a factor (cattle = 0.7, sheep = 0.1, goats = 0.1 and poultry = 0.01).

regression above were used as basis for classification. Fuzzy k-means classification as described by Salasya and Stoorvogel (2010) using the fclust package in R (Ferraro et al., 2019) was used to form clusters according to minimized Euclidean distances within farm typology groups. These farm types were then characterized by testing for differences in ONS allocation and social connections related to ONS information, by using ANOVA and Fisher's exact tests where a $p < 0.05$ was considered significant. Between-Class PCA (BCA) was used to to determine possible group distinction following characterization into typologies using the ade4 package (Bougeard and Dray, 2018) and overall significance differences among classes determined with a *post-hoc* Monte-Carlo test.

RESULTS

Focus Group Discussions

Relevant quotes from the focus group discussions illustrate broadly how farmers consider the themes of crop residue and manure allocation, gender responsibilities and trade-offs in ONS management (**Table 5**). Overall, the farmers in Nandi and Vihiga, and to a lesser extent Busia, placed value on feeding the livestock over returning residues to the plots (Quotes 1 and 2) because they prioritize livestock and the resulting value from selling milk (Quotes 8 and 9). Other tradeoffs in residue allocation result from alternative household uses such as burning of legume residues for salt (a special ash used in the cooking of traditional vegetables

TABLE 4 | Dependent and predictor variables that were used for stepwise regression and stepwise multinomial logistic regression.

Variable type	Group	Information asked from interviewees.
Predictor	Socio-economic	Livestock ownership (TLU* per household)
		Area of main plot (ha)
		Tenure of main plot (owned vs. rented or shared)
		Main source of labor (hired vs. household members)
		Food sufficiency (months yr $^{-1}$)[‡]
		Crop residue main use (feed livestock/retain infield/compost/burning)
		Mineral fertilizer use (Yes/No)
		Family size
		Education level of household head (none, primary, secondary, vocational/tertiary)
		Gender of household head
	Socio-cultural	Number of trainings in soil fertility management attended (in the past 5 years)
		Number of times the farmer has been visited by extension workers in the past year
		Number of farm groups they belong to
		Frequency of consulting other farmers on soil fertility management (contacts per season)
		Adherence to perceived social norms of crop residue management (Yes/No)
	Environmental	Location (agroecological zones)
		Perceived soil fertility status of main vs. secondary cropping plots[ƛ]
Response	Allocation and use of organic inputs to the main plot[†]	% of crop residues retained (continuous)
		% of cattle manure (composted, uncomposted, and combined) applied (continuous)[**]
		% of poultry manure applied in-field (continuous)
		Main use of crop residues (categorical)

**Livestock ownership was converted to Tropical Livestock Units (TLU) by multiplying the number of livestock owned by a factor (cattle = 0.7, sheep = 0.1, goats = 0.1, and poultry = 0.01).*

[‡] *Farmers where asked how many months in a year that they felt they had enough food to feed their household comfortably with 3 meals a day.*

[ƛ] *Soil fertility status refers to the main plot vs. the secondary plot according to the farmer's perception, main plot usually perceived as more fertile.*

[†] *The study concentrated on the allocation of ONS to the main plot because half of the farmers did not have a secondary plot and of those that had, less than half applied any ONS to it.*

***We looked at 3 dependent variables for cattle manure allocation as is normally done in the 3 areas (i) adding cattle manure to compost and/ or composting it before applying to the field (composted cattle manure) and (ii) applying it to the field directly without composting (uncomposted cattle manure) (iii) combining the composted and uncomposted cattle manure (combined cattle manure).*

TABLE 5 | Farmer quotes on organic nutrient source management, responsibilities and trade-offs following focus group discussions in Nandi, Vihiga and Busia counties in western Kenya in July 2018.

Theme	Focus group quotes exploring the theme
Crop residue and manure allocation	1. "We believe in letting the farm feed the cattle and the cattle feed the farm" Nandi farmer
	2. "I prefer feeding our livestock first and what remains I can take to the field" Vihiga farmer
	3. "Some of us may consider applying manure only in sections that have shown good yield potentials and ignore other sections"
Gender responsibilities in ONS management	4. "The decision on how maize stalks are used is usually made by the male members of the household as they value their livestock and believe that all cattle belong to them"
	5. "The decision to burn legume residues is usually made by female members of the household"
	6. "Female farmers determine the use of bean residues and they burn them to make salt"
Trade-offs in ONS management	7. "We burn legume residues for cooking traditional vegetables or we can sell the ash for 200 shillings/20 kg bag."
	8. "I can exchange maize stalks for milk"
	9. "I can fetch more money from selling milk, so I prefer giving the residues to my livestock"
	10. "There are farmers who are very old and cannot carry the residues home to feed animals and therefore leave them on the farm or sell them, a bundle of maize stalks sells for 50 shilling (equivalent to 50 cents United States Dollars)"

and meat preservation; Quotes 6 and 7). Management of ONS is determined by gender, especially for legumes, where female members of the household were responsible for management of crop residues (Quotes 5 and 6), while a few farmers stated that maize stalks are mainly managed by male members of the household (Quote 4). In Busia, older farmers preferred to leave residues in the plot or sell them *in situ* to the few farmers without their own, as they see it as laborious to carry the stalks home (Quote 10).

General Management of Organic Nutrient Sources

The most fertile plot according to the farmers' perception was defined as the main plot and the less fertile plot was defined as

TABLE 6 | Characterization of farming systems and organic input use in the main plots vs. secondary plots in smallholder systems from western Kenya.

		Main plot ($n = 184$)	Secondary plot ($n = 102$)	*p*-value
Plot size (ha) *mean (se)*		0.45 (0.48)	0.27 (0.29)	0.001*
Tenure	Owned	83%	73%	0.001*
	Rented/Shared	17%	27%	
Main farming system	Mixed/intercropping	75%	40%	0.004‡
	Sole cropping	24%	46%	
	Fallow	1%	14%	
Organic input use in plot	Yes	78%	44%	0.005‡
	No	22%	56%	
Average yield-2018 long rainy season (Mg ha^{-1})	Maize	1.03	0.44	0.001*
	Beans	0.44	0.46	0.04*

p-values for differences between means of the main and secondary plots are shown in the far-right column.

**p-values for t-tests between the main plot and secondary plot means.*

‡p-values for Fisher's Exact tests for differences in proportion between the main and secondary plots variable levels.

the secondary plot. About half of the of the households surveyed (56%) had a secondary plot in addition to the main plot, with the others just managing a single plot. There was large variability in plot size for both main and secondary plots, but landholding was generally small, with an average plot size of < 0.5 ha for both plot types (**Table 6**). Most plots were owned by the household, but a higher proportion of the secondary plots were shared or rented than for main plots. Plot designation influenced management, such that the main plot used intercropping or mixed cropping systems and the majority had ONS applied to them (**Table 6**). In contrast, there were more secondary plots that were sole cropped (46%) or that were left fallow (14%) compared with intercropping/mixed cropping (40%). Farmer reported maize yields for the 2018 long rainy season were significantly higher in the main plots than the secondary fields, while beans yields were marginally higher in the secondary plot (**Table 6**).

Consistent with our focus group findings, maize crop residues produced from the plots were mainly fed to livestock (by 53% of households) or retained in-field (by 33% of households). A few farmers (8%) added the residues to compost and 8% of households had no residues at all due to crop failure. Other uses of crop residues such as burning of legume residues for salt (76% of households that grew legumes) or burning in-field in the case of cereal residues (2%) were noted. Regarding composting, 61% of farmers owned a compost or farmyard manure pile composed of all their manure or a selection of manure, crop residues, ash, kitchen waste, while 39% had no compost pile of any form. Other ONS such as biochar and *Tithonia diversifolia* were mentioned by only 5% and 7% of farmers, respectively, who added these as well as leaf litter from the nearby trees and forest to their compost/farmyard manure.

Gender and Organic Nutrient Source Management

The general allocation and management responsibility of organic resources by gender depended on the type of ONS (**Figure 2**). Generally, more households had their ONS managed by female members of the household compared males. Responsibility between genders differed slightly with animal manure, maize residues, and compost/farmyard management (**Figure 2**). However, management of legume residues was mainly the responsibility of the female household members (57% female vs. 23% males: $n = 160$ households). Allocation of poultry manure to the main plot was significantly higher in male headed households (mean± standard error: $55 \pm 6.7\%$; $n = 137$) than female headed households ($39 \pm 3.9\%$; $n = 46$).

Zone to Zone Variation in Organic Nutrient Source Allocation

The main use of crop residues differed by location ($p < 0.001$), where the number of farmers in Busia who retained their crop residues in-field was 3 and 4 times higher than in Vihiga and Nandi, respectively (**Figure 3**). Farmers in Nandi and Vihiga were more likely to feed crop residues to livestock than retain them in the field. The proportion of crop residues allocated to the main plot vs. other fates also differed between locations ($p < 0.001$; **Table 7**). Crop residues retained in the main plot were significantly influenced by location, where farmers in Busia retained on average twice the amount of residues in the main plot ($67.33 \pm 4.53\%$) plot than that observed in Nandi and Vihiga ($39.9 \pm 3.5\%$; $29.51 \pm 3.73\%$). There were also significant differences in the proportion of composted cattle manure allocated to the main plot in the three locations ($p = 0.01$; **Table 7**) with farmers in Busia and Vihiga allocating a higher proportion of the manure produced to the main plot ($51.3 \pm 5.4\%$, $49.8 \pm 5.3\%$ vs. $32.3 \pm 5.3\%$ in Busia, Vihiga, and Nandi, respectively).

Resource Endowment Factors

A variety of farm resource indicators influenced allocation of ONS to the main plot as an indicator of nutrient management strategies (**Table 7**). For example, farms with greater numbers of livestock (TLU) allocated significantly more composted and combined cattle manure to the main plot ($R^2 = 0.08$; $p = 0.001$ and $R^2 = 0.14$; $p < 0.001$, respectively), than those

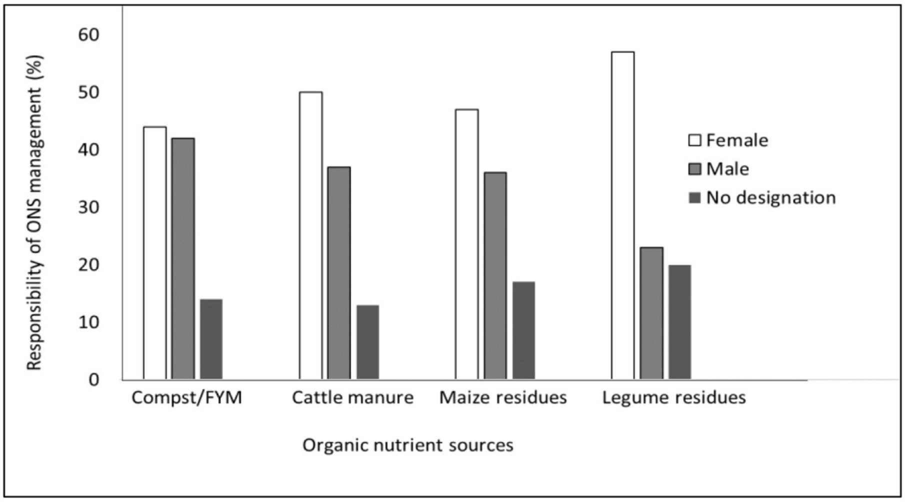

FIGURE 2 | Management responsibility of organic nutrient sources separated by gender in households of Busia, Nandi, and Vihiga counties in western Kenya. Number of households producing compost/Farmyard manure(FYM) = 113; number of households with Cattle manure = 167; number of households with maize residues = 180; number of households with legume residues = 160.

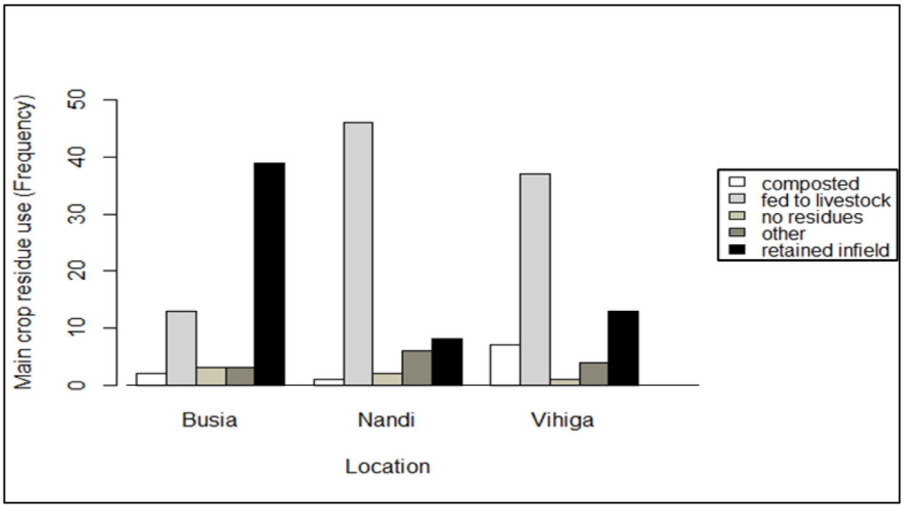

FIGURE 3 | Frequency of the farmers in Busia, Nandi, and Vihiga counties in western Kenya who allocate crop residues produced from their main plot for to a variety of different uses.

with fewer livestock. Households that were more food secure (i.e., those that indicated having enough to feed their families comfortably 3 meals a day for 12 months) applied significantly less uncomposted cattle manure (average proportion allocated to the main plot = 22% ± 5.3; $n = 33$) compared to households that were less food secure (average proportion allocated to the main plot 51% ± 7.33; $n = 36$; $p = 0.02$; **Table 7**). Regarding land tenure, farmers who rented or shared plots retained significantly more residues (owned 39.28% ± 2.76 vs. shared/rented 59.03% ± 6.3: t-test $p = 0.006$) than those who owned their main plots. Area of main plot influenced manure applied, in that plot size decreased marginally with increase in cattle and poultry manure allocated.

Socio-Cultural Factors as Drivers of ONS Management

Adherence to social norms helped to explain some of the variability in ONS management (**Table 7**). However, adherence to norms of crop residue management appeared to depend on location (adherence to norms by location interaction: $p = 0.04$; **Table 8**). Overall, farmers who indicated adherence to social norms of crop residue management in Vihiga retained

TABLE 7 | Farm-level predictors selected using a stepwise regression that explain variation in the proportion of crop residues retained, cattle and poultry manure applied to the main plot in Nandi, Vihiga, and Busia counties of western Kenya.

Dependent variable	Predictor variable in final model*	η^2	*p*-value
Proportion of crop residue left in main plot	Location	0.24	<0.001
	Adherence to norms (residue)	0.04	0.04
	Tenure (main plot)	0.04	0.002
	Area of main plot (ha)	0.02	ns
Proportion of composted cattle manure allocated for use in main plot	Location	0.05	0.01
	Number of animals (TLU)	0.06	0.001
	Extension visits	0.08	0.002
	Area of main plot (ha)		ns
Proportion of uncomposted cattle manure allocated for use in main plot	Area of main plot (ha)	0.02	0.03
	Labor (hired vs. household members)	0.08	ns
	Months secure‡	0.11	0.002
	Adherence to norms (of composting)	0.05	0.04
Proportion of cattle manure (composted plus uncomposted) allocated for use in main plot	Number of animals (TLU household^{-1})	0.17	<0.001
	Labor (hired vs. household members)	0.04	0.08
	Education	0.04	0.07
	Area of main plot (ha)	0.05	0.02
Proportion of poultry manure allocated for use in main plot	Gender	0.02	0.04
	Area of main plot (ha)	0.02	0.09

Data was collected from 184 households in June of 2019.

**Are predictor variables selected in the final model following stepwise regression analysis. TLU are Tropical Livestock Units (TLU).*

‡Farmers were asked how many months in a year that they felt they had enough food to feed their household comfortably with 3 meals a day.

η^2 *is the proportion of variance explained by each predictor variable; ns means not significant.*

TABLE 8 | Percentage of total crop residues retained, and total uncomposted cattle manure applied to the main plot as influenced by adherence to social norms in three counties of western Kenya (Nandi $n = 62$ and Vihiga $n = 62$; Busia $n = 60$).

Location	Crop residues retained			Uncomposted cattle manure		
	% average proportion applied to main plot					
Adherence to norms of ONS management						
	No	Yes	Not Sure	No	Yes	Not Sure
Busia	74.4 (6.75)^{d}	65.2 (6.73)^{cd}	50.0 (13.09)^{abcd}	57.8 (12.94)^{b}	18.3 (8.10)^{a}	31.9 (9.71)^{ab}
Nandi	27.7 (8.06)^{ab}	33.5 (3.68)^{ab}		37.8 (12.94)^{b}	40.0 (11.71)^{a}	42.4 (7.21)^{ab}
Vihiga	45.6 (7.07)^{bc}	19.1 (3.04)^{a}		100 (38.8)^{b}	26.2 (7.21)^{a}	26.7 (8.47)^{ab}
p values		*Adherence: $p = 0.003$* *Location: $p = <0.001$* *Adherence x Location: $p = 0.04$*			*Adherence: $p = 0.04$* *Location: ns* *Adherence x Location: ns*	

Means connected by the same letter are not significantly different using Tukey's HSD pairwise comparisons. Numbers in parenthesis are the standard error of the mean.

significantly less residues in the main plot than those who did not adhere to norms, which reflects the more common practice of retaining few residues in-fields there, in favor of feeding to livestock. The few farmers who did not adhere to perceived social norms of crop residue management in the three locations explored other options of crop residue management namely composting (5% of farmers) and other uses such as burning, selling main and transferring to other plots (7% of farmers).

The proportion of uncomposted cattle manure applied to the main plot was significantly related to adherence to social norms of composting ($p = 0.04$; **Table 7**). Households that did not adhere to social norms of composting (i.e., not composting manure before application) applied more uncomposted cattle manure (average proportion applied to main plot 52% ±10.6; $n = 19$) compared to those that were not sure of composting norms (average proportion applied to main plot: 36% ± 4.9; $n = 64$) and those who adhered composting norms (average proportion applied to main plot: 25% ± 4.7; $n = 62$).

Extension visits were significantly correlated with the proportion of composted cattle manure allocated to the main plot ($p = 0.002$; **Table 7**). Overall, farmers who had never been visited by extension (99 out of 184 farmers) allocated ~1.5 times less composted cattle manure than those who had interacted with extension at least one or more times. The same trend was noted when the data was disaggregated into counties (**Figure 4**).

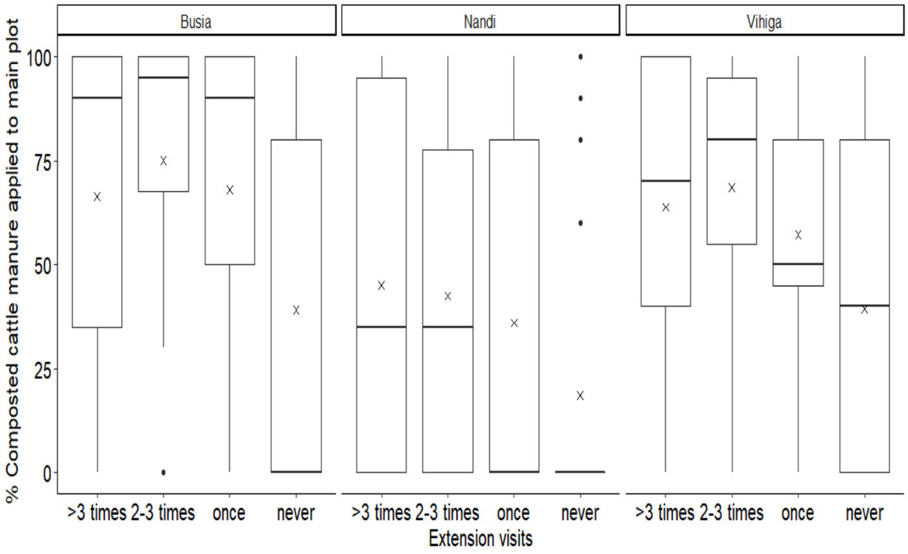

FIGURE 4 | The percentage of composted cattle manure applied in farmers' main plot as influenced by the number of interactions with extension agents in Busia, Nandi, and Vihiga counties in western Kenya. Box plots show the spread the data points for each group, while the mid-line represents the median of each group and x indicates the group mean.

TABLE 9 | Constructed farm typologies using fuzzy k-means classification for organic nutrient sources allocation across 184 farming households Nandi, Vihiga, and Busia counties in western Kenya.

Farm type	*n*	Description
1	28	**Resource endowed** Farmers with livestock in forms of cattle and poultry (Tropical Livestock Units-TLU >3); have relatively larger pieces of plots (>0.4 ha). Some farmers have good interactions with extension over 3 times in a year, but some were never visited by any extension member. They tend not to be clearly influenced by social norms of crop residue management.
2	19	**Non-adherent and well-connected** Farmers with livestock ownership of TLU between 1.5 and 3. They have smaller plot size area of the main plot about, 0.4 ha. The farmers tend not to adhere strongly to social norms of crop residue management and have had frequent interactions with extension (more than two times the previous year)
3	93	**Adherent and less connected** Farmers with few to no livestock (average TLU of <1.5) The land sizes are very small (<0.4 ha). They adhere strongly to social norms of management and most have little to no interaction with extension workers.
4	44	**Least resource endowed** Farmers with few to no livestock (average TLU of <1) The land sizes are very small (<0.4 ha). They do not adhere strongly to social norms of management and most have never been visited by extension workers before.

Descriptions are provided for each type based on mean values of farm resource endowment, adherence to norms of organic nutrient sources practices, and connectedness to information sources for organic nutrient sources management practices.

Organic Nutrient Sources in Relation to Farm Typology

There were six ONS management clusters formed from the surveyed farms using fuzzy k-means classification (silhouette width = 0.60, lowest average membership degree = 0.88). These were then further grouped into four types by merging two of the pairs of clusters that had the shortest Euclidean distance (**Table 9**). The majority of the farmers (72%) were in the less resource endowed and less connected farm Types 3 ($n = 92$) and 4 ($n = 44$).

When examining differences between the farm types, there were no significant differences in the average total maize residues produced; however, Type 1 (Resource endowed) farmers produced the highest yield (1.04 Mg ha^{-1}) and Type 4 (Least resource endowed) farmers the lowest (**Table 10**). Similarly, farm type had no influence on the proportion of maize residue retained to the main plot, but Type 1 and Type 4 farmers retained a higher proportion of residues infield while Type 2 (Non-adherent and well-connected) and Type 3 (Adherent and less connected) farmers retained less residues infield.

TABLE 10 | Mean total organic inputs by farm type produced by farming households ($n = 184$) during a typical long rainy season in western Kenya.

		Organic inputs			Proportion allocated to main plot			
Farm type	**Average size of main plot**	**Crop residues (maize)**	**Cattle manure**	**Poultry manure**	**Crop residues (maize)**	**Composted cattle manure**	**Uncomposted cattle manure**	**Poultry manure**
	ha	***Mg ha^{-1} long season^{-1}***	***kg DM farm^{-1} long season^{-1}***		***% of total organic resources allocated to the main plot***			
1	0.98 (0.16)^{b}	1.04 (0.11)	1 639 (203)^{a}	174 (37.1)	54.8 (6.48)	42.4 (7.94)	26.5 (7.62)^{ab}	31.0 (8.48)^{a}
2	0.47 (0.08)^{a}	0.86 (0.18)	740 (257)^{b}	158 (38.1)	37.4 (8.00)	31.6 (9.8)	58.1 (9.91)^{b}	62.1 (10.48)^{ab}
3	0.35 (0.03)^{a}	0.75 (0.75)	794 (113)^{b}	106 (18.9)	38.3 (93.62)	48.3 (4.43)	28.5 (4.51)^{a}	51.1 (4.73)^{ab}
4	0.35 (0.05)^{a}	0.68(0.14)	745 (164)^{b}	85 (26.6)	45.9 (5.26)	42.7 (6.65)	35.9 (6.86)^{ab}	60.2 (6.88)^{b}
p-value	*<0.001*	*ns*	*0.002*	*ns*	*ns*	*ns*	*0.04*	*0.04*

Values are reported for the proportion of crop residues retained, as well as cattle manure (composted and uncomposted) and poultry manure applied to the main plot. Numbers in parentheses are the standard error of mean. P-values are report difference between the different farming household typologies, while means followed by different letters are significantly different from each other according to Tukey's HSD pairwise comparisons.

Type 1 farmers had significantly more estimated manure production per season (1,639 kg season^{-1}) compared to all the other farmers (**Table 10**). The proportion of composted cattle manure and combined cattle manure applied to the main plot did not significantly differ with type but followed the order Type 3>Type 4≥Type 1> Type 2 and Type 2>Type 3>Type 1≥ Type 4, respectively. However, the proportion of uncomposted cattle manure was significantly higher ($p = 0.04$) in Type 2 farmers, followed by Type 4 and Type 1 and 3 farmers had the least proportion allocated to their main plot (**Table 10**).

Small quantities of poultry manure were produced by farmers and did not differ significantly among types (**Table 10**). Nevertheless, there were significant differences in percentage of poultry manure applied in the main plot ($p = 0.04$), in which Type 2 and 4 farmers had higher average proportions allocated to the field (mean 62.1 and 60.2%, respectively), than Type 3 and Type 4 farmers (mean = 51.6 and 31%, respectively).

There were significant differences in the socio-cultural interactions of farmers by farm type with regards to obtaining information on soil fertility and ONS management. Training of farmers in areas of soil fertility (in workshops or field days) and ONS management was significantly different with farm type (Fisher's exact test $p = 0.01$). Type 2 farmers were the most trained with at least 89% of farmers having received some form of training. This was followed with type 1 (57%) and type 3 (54%) farmers. Type 4 farmers were the least trained with just 41% of them having received formal training at least once since they started farming.

Belonging to farmer groups (where farmers from the same community come together to learn from each other and or pool produce for marketing amongst other reasons) was significantly different among farmer types (Fisher's exact test, $p = 0.02$). Type 1 and 2 farmers were more likely to belong to farmer groups, with 61 and 88%, respectively, belonging to at least one farmer group. Most Type 4 farmers (66%) did not belong to any farmer group. 52% of Type 3 farmers belonged to at least one farmer group.

Consultation with other farmers on issues concerning soil fertility and organic nutrient sources management was significantly different with type (Fisher's exact test $p = 0.03$). Type 2 farmers were the most interactive, with at least 56% of the farmers having consulted other farmers at least once in the season. This was followed by Type 3 farmers (36%), Type 1 farmers (29%) and lastly only 13% of Type 4 farmers consulted other farmers at least once in the season.

Between class analysis (BCA) showed that the first two axes of variation encompassed 85% of the variability in the chosen set of descriptor variables for farms (**Figure 5**), and highly significant differences among the four farmer types (Monte-Carlo test $p = 0.001$). Nevertheless, there was some overlap between farm types (**Figure 5**), such that farm Type 1 is clearly separated from the other three types in that on average they have more livestock and a larger area of land. There is a subtle distinction between Types 3 and 4, as Type 3 are more adherent to residue management and are bit more likely to be in Nandi than Type 4. Finally, Type 4 allocate more poultry/manure than other types.

DISCUSSION

Our results showed that the main determinants of ONS management in these mixed crop-livestock systems of western Kenya were environmental (agroecological zone context and perceived soil fertility), resource endowment (TLU, area, months food secure and tenure of plot) as well as socio-cultural (adherence to social norms and interaction with extension). Additionally, we note that responsibilities in management and allocation of ONS were gendered for some resources (e.g., legume residues), and also show a general trend of women overseeing most ONS. These findings thus lend support to existing frameworks on allocation of ONS management in smallholder systems that have placed emphasis on resource endowment as a major determinant of ONS management (Mugwe et al., 2009; Andrews et al., 2013; Ajayi and Solomon, 2017), but also indicate some divergent or interesting additional patterns in allocation of ONS in smallholder farms of this region.

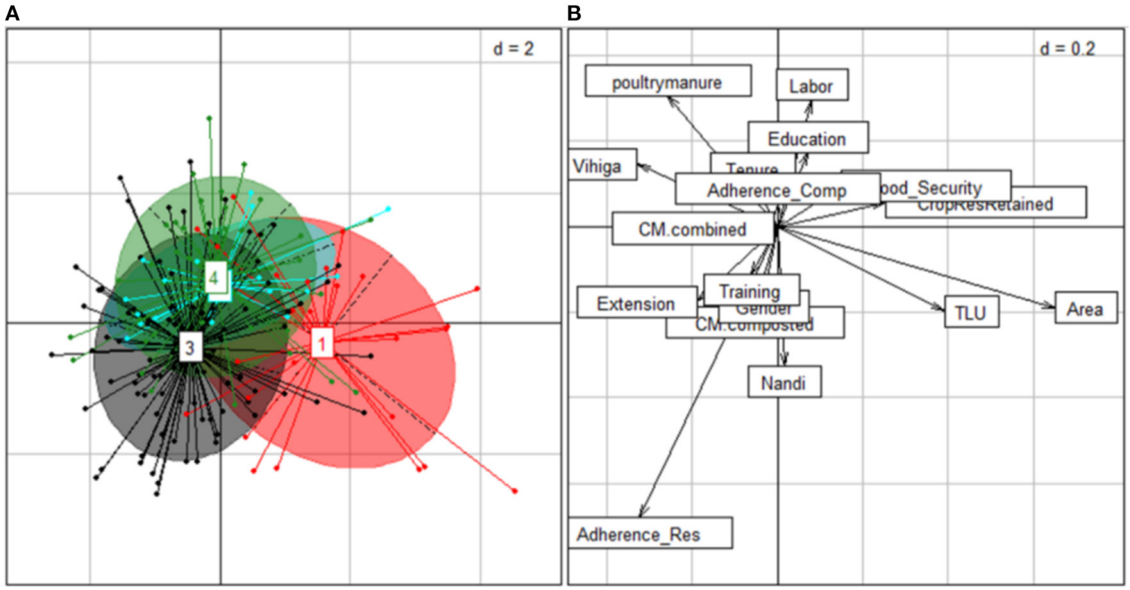

FIGURE 5 | Between class analysis (BCA) showing group separation [**(A)** group classes and **(B)** arrow linking points to origin] for constructed farm typologies in organic nutrient sources management in three counties in western Kenya. The groups 1–4 are constructed farmer types of ONS management (see **Table 9**). TLU is Tropical Livestock Units; Area is area of main plot; Nandi/Vihiga are counties in western Kenya; Education is the education level of household head; CM, combined; CM, composted and Crop; Res, Retained; represent the proportion of cattle manure not composted and composted and crop residues that were allocated to main plot, respectively; Adherence_Res and Adherence_Comp refers to adherence to social norms of crop residue and compost management, respectively; Extension is the number of times a farmer had interactions with extension agents in the previous year; Food-Security refers to how many months in a year that farmers felt they had enough food to feed their household comfortably with 3 meals a day. Labor represents main source of farm labor (hired /household members). Training is the number of formal trainings in soil fertility management attended by the farmer in the past 5 years.

Household Members, Gender, and Management of ONS

In most households, female members were the ones responsible for managing and allocating resources such as compost, maize residues, and animal manures. Management of legume residues, moreover, was clearly a female household member's responsibility (Quotes 4, 5, and 6; **Table 5**; **Figure 2**). Women manage most of the growing and post-production handling of legume crops as they are generally considered a "woman's crop" due to lower value compared to maize (Ferguson, 1994). Women farmers have been noted to have an interest in diversifying cropping systems with legumes because of their nutritional value, since they are typically responsible for preparing meals for families (Snapp et al., 2019). This generally aligns with other studies showing how women's role of providing and making food for the family influences their choices regarding use of household resources available to them (e.g., DeVault, 1994). This can also explain the choice of burning of residues over other uses such as retaining the residues infield, since legume residues are also used for the production of "salt" that can be used to preserve meat for traditional meals, or it can be used as a feed supplement for cattle. Clearly then, understanding gender factors that influence the fate of legume residues is crucial, especially in light of the fact that these residues are often promoted to improve soil health and crop yields (Ojiem et al., 2014; Smith et al., 2016). Further, we note that engaging only with males in households regarding the benefits or challenges of legume residue management is likely to be far less effective than engaging with women. Overall, this finding shows how use of legumes, and alternative uses including as ash for salt, has important economic and cultural value, and this should be considered as a determinant of ONS allocation.

Spatial Variability at Different Scales: Zone to Zone and Within-Farm Variability of ONS Management

Agroecological factors or what Liu et al. (2018) called "macro factors" that form the common management backdrop for a large number of farmers in one region vs. another, often influence the allocation of organic resources within a smallholder farm. In our study, it is likely that the strong effect of location on ONS management was mediated by a range of climatic conditions and soils which determine the type of farming systems possible, and in turn, determines the type and amount of organic resources that are produced on a farm (Pedzisa et al., 2015; Rusinamhodzi et al., 2016). In our study, Nandi (at high elevation and medium rainfall) had a lower proportion of residues retained in-field than Busia (at low elevation and lower rainfall). This is likely related to the fact that Nandi is located at higher altitudes and more intensive, zero-grazing dairy farming is more common due to a climate that better supports dairy production. As such, the farmers there require feed to be harvested and carried from the fields to the cattle pens after harvest to supplement animal feed. In Busia, however, it is the common practice to retain crop residues in the field since animals are mostly open grazed rather than pen fed. Similar to Nandi, Vihiga (medium elevation, high rainfall) is higher in elevation and has more intensive farming systems than in Busia but retains slightly less residues in-field.

In addition to this zone-level variation, within farm spatial gradients also affected nutrient management, by which farmers prioritized ONS allocation to main plots over secondary plots. While the less productive plots do receive their own residues, they tend to have lower productivity and thus lower residue biomass inputs than the main plots. Such management gradients likely lead to heterogeneity in soil fertility within farming systems, where the plots closer to the homestead (usually the main plot for security reasons, ease of manure or compost application, or other conveniences) typically have higher fertility. This aligns well to other studies in which farmers concentrate their organic resources on main or favored fields, even if it might be more productive to distribute a greater proportion of their ONS to less productive fields (Mtambanengwe and Mapfumo, 2005; Tittonell et al., 2005; Masvaya et al., 2010; Giller et al., 2011). The type of crops grown in the plot also influences the proportion of residues retained or taken away from that plot. For example, since legumes are mostly grown in the outfields/secondary plots, and legume residues are burnt off field to be used in the homestead for salt or cattle licks, they often do not contribute much to soil fertility save for a minor contribution through root biomass.

Resource Endowment Factors Affecting ONS Management

Farmer resource endowment proxies, namely livestock ownership (TLU), food security and to a lesser extent, area of the main plot, were among the main determinants of use and allocation of ONS. Resources positively influenced the proportion of ONS allocated to the main plot in that the more livestock or land area a farmer has, the more organic resources are produced on farm and these will be likely returned to the plots as crop residues or manure. This suggests that positive relationships between the proportion of crop residues applied to main plot and manure used and TLU or area of land in these systems could be a direct influence of an increased amount of ONS that are available in the farms with more livestock and larger areas rather than an ability to get external mineral fertilizer resources. This contrasts with another pattern we might expect, which is that wealthier farmers would be using more agrochemical inputs (i.e., fertilizers) and that reliance on ONS would decrease when one has the ability to buy synthetic inputs. We also noted a pattern with cattle manure where households that relied on the female members of the household for management of ONS applied less cattle manure to their plots compared with those households that were able to hire labor in cash or in kind (more resource endowed farmers). Ability to hire external labor is also a proxy for resource endowment in smallholder farming systems (Grabowski and Kerr, 2014).

We noted that farmers who rent or share land allocated a slightly higher proportion of residues back to the main plot compared to those who owned land. One possible explanation for this is that transporting residues from the plots is costly if the rented or shared plot is not near the homestead; alternatively returning residues to the field may be a condition for renting the land. Another reason for this could be that if a renter shows interest to improving soil fertility, they might secure a long-term lease from the owner due to the trust thus gained from the owner (Neef, 2001). Renters retaining greater amounts of residues is contrary to some studies that suggest that farmers who rent or share land do not adopt practices that can improve that land if the resource requirement to do so is high. This is because they consider the need to maximize on the investment that they use in paying rent of land they do not own (Adjei-Nsiah et al., 2004; Fraser, 2004; Lawin and Tamini, 2019). Others have shown land tenure not to significantly influence the amount of organic inputs applied in the plots (Leonhardt et al., 2019), suggesting that the relationship between land tenure and residue return to soils is complex and may vary region-to-region in connection with the macro factors discussed above.

Socio-Cultural Factors in Management of ONS (Extension and Adherence to Norms)

Farmers who interacted with extension workers at least once in the 2018 farming year applied more composted cattle manure to their main plot as compared to those that had no interaction at all. The link between extension visits and manure application is consistent with the important role that extension has been seen to play in influencing on-farm innovation beyond research in both developing and developed communities (Takahashi et al., 2020). In their study of utilization of soil conservation practices, Faniyi et al. (2019) noted that there was a correlation between contact with extension and use of innovations. For farmers to decide to allocate ONS resources (or not) to a plot, they need to be adequately aware of the potential tradeoffs. This awareness can result from interactions with extension, so that the frequency of interactions with extension workers during farm visits or training influences their knowledge about soil fertility management (Pedzisa et al., 2015; Ajayi and Solomon, 2017). If extension workers are not trusted by a population of farmers, the knowledge sharing simply will not work because the social relations are not conducive to having that knowledge "stick." To put it simply, trust helps makes knowledge (and technology) transfer possible (Carolan, 2006). This underscores the value of including socio-cultural variables into a study such as this.

In contrast to these extension knowledge flows from outside the community, farmers' awareness of and adherence to social norms are a parallel source of knowledge, potentially influencing a farmer to keep with community ideas of how ONS are managed (Daxini et al., 2018; Liu et al., 2018). In Vihiga, where the norm is to retain fewer crop residues in-field and feed more to livestock, farmers who adhered to social norms retained few residues in their field. Moreover, in all counties, farmers who adhered to social norms of composting (i.e., not composting) applied more uncomposted manure directly to their plots than those who did not. This can be explained in that, as with many other aspects of farming practices, how resources are used also hinges on the awareness a farmer has on how other farmers manage their resources and may follow suit because, as one farmer commented during the focus group discussions "this is what we normally do in this community." This relatively widespread awareness of norms is consistent with the idea that pressure not to deviate from norms can influence farmers to follow a certain way of managing ONS even though they might think it is not the best way to do so (Lalani et al., 2016). Nevertheless, some non-adherence to norms suggests both the influence of past training and extension efforts as well as innovation potential of farmers and variability that can be a strength when thinking of endogenous innovation and farmers' ability to adapt. Across all regions, farmers who adhere to social norms of crop residue management tend not to experiment as much with other ONS strategies such as biochar, *Tithonia diversifolia* or composting. These farmers may benefit from training and education on alternative approaches to ONS management and potential benefits.

Typologies for ONS Management and Implications

While ONS allocation and use differed according to farm type, overall ONS produced on all farm types was low as evidenced by the low total maize residues and manures produced due to low livestock ownership. In addition, the actual amounts allocated per unit area may not significantly differ among farm type but the decision to allocate a certain proportion to the field differed was influenced by type. Moreover, if we consider significant losses that may occur during management and grazing (Rufino et al., 2007), these soils are likely to become more nutrient depleted if no supplementary nutrients are added to the farm from exogenous sources. This nutrient depletion will likely lead to continued food insecurity countering efforts to eliminate zero hunger.

Despite resource endowment generally leading to more resources being applied as previously shown, the typology classification indicated that what is driving ONS allocation is not just resource availability, but also other factors such as norms and connections. This is seen in that one would assume that Type 1 farmers who are more resource endowed (as evidenced by the average total inputs produced) linearly applied more animal manure in their fields because they have more livestock that produces manure. However, it is Type 2 (Non-adherent and well-connected) farmers that allocate more ONS than other groups. This may be since they are the most trained in areas of soil fertility management and have more interaction with other farmers than Type 1, Type 3 (Adherent and less connected) and Type 4 (Least resource endowed) farmers. They are also well-connected with extension agents and have the resources (after Type 1) in terms of organic inputs. They may therefore represent "experimenter farmers" and are likely to adopt and adapt to diverse ways of managing ONS, in accordance also with the fact that not following norms can be considered as indicating the capacity to innovate. This group can be leveraged as "lead farmers" who work with development organizations for farmer-to farmer extension (Franzel et al., 2014; Fisher et al., 2018). Type 4 together with Type 3 farmers allocate more poultry manure to the field than Type 1 and Type 2 farmers—signifying the importance of poultry manure within this group. The need to utilize every resource they have might drive importance placed on poultry manure compared to Type 1 and 2 where other resources that are available in larger quantities tend to be more important.

We note that even within the typologies there is high variability of ONS allocation and overlap between types, as shown in the between class analysis (BCA). Farm types had a limited ability to explain variability and seemed to be structured mainly along the lines of resource endowment; however, the typologies developed provided important insights regarding farmers' access to networks, organizations, and extension. In summary, smallholder systems are complex and share some basic characteristics of ONS allocation to fields. This is important, as targeted training may yield better results for soil fertility management (Chikowo et al., 2014). As such, targeting farm types rather than individual farmers for practices to improve allocation of organic inputs for soil fertility might be a way to cater to the diversity of the farmers in these systems (Rusinamhodzi et al., 2016).

CONCLUSIONS

Our findings indicate that beyond resource endowment (livestock, land area, labor), additional factors of location, perceived soil fertility of a plot, gender, norms, land ownership, and networks all influence the allocation of ONS to plots. Organizations and extension agents working with farmers on soil fertility management should thus consider these factors and tailor their technologies, trainings, and capacity building efforts in a way that better recognizes the drivers of ONS use. This suggests an "options by context" approach where ONS strategies target different communities based on the preference, norms and farming systems of each community, as opposed to applying a "blanket" approach for all zones. Additionally, since management of legume residues was strongly gendered, engaging with women farmers on options for improved legume residue management is fundamental for developing effective soil fertility management strategies. While typologies were mainly based on resource endowment and offered limited ability to explain variability in resource management, this approach provided important insights about networks, extension, and training within types. Importantly, socio-cultural factors that encourage use of organic inputs such as enhanced connections with farmers through extension, farm groups and peer interaction should be championed if efficient ONS cycling is to happen on farm.

This study advanced our understanding of the factors affecting ONS management in smallholder systems, but future research is needed to explore how this translates in terms of quality of ONS added, nutrient mining, long-term nutrient balances, and the implications for soil health. For example, relating the farm types in different locations and patterns of allocation to actual outcomes of nutrient and soil carbon cycling would be a useful next step in understanding more generally the socio-economic factors that drive sustainability of soil management on smallholder farms globally.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Colorado State University Institutional Review Board. The patients/participants provided their written informed consent to participate in this study.

AUTHOR CONTRIBUTIONS

BN-M, SV, and SF conceived of the presented idea. BN-M developed the instruments with the contributions from MC and JO. BN-M analyzed the data with contributions from SV. SF supervised the findings of this work. All authors discussed the results and contributed to the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.692981/full#supplementary-material

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Assessing the Circularity of Nutrient Flows Across Nested Scales for Four Food System Scenarios in the Okanagan Bioregion, BC Canada

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In light of continued nutrient pollution in water bodies and anticipated insecurities related to future nutrient supplies, there is an increasing awareness of the need to use nutrients in a more circular way. As part of a food system design study in the Okanagan bioregion, BC Canada we set out to evaluate different food system scenarios for the year 2050 in terms of nutrient circularity. In doing so, the objective was to evaluate the circularity of nutrient flows not only in the Okanagan, but also in relation to exogenous regions, insofar as nutrient flows relate to feed and food consumption and production in the Okanagan. This is important because feed and food trade means that nutrient inputs to crop production in the Okanagan may make their way into organic residuals outside the Okanagan, and *vice versa*. If not accounted for, this may lead to a distorted picture when analyzing nutrient circularity. To this effect, we applied an analytical framework and calculation model that explicitly tracks nutrients from crop production to organic residual generation. The results of the study suggest that assessing nutrient circularity across nested scales was critical for two reasons. First, changes in overall nutrient flows in response to population increase and dietary change were found to be more pronounced outside the Okanagan. Second, our analysis clearly revealed the extent to which feed and food trade boost nutrient self-reliance in the Okanagan at the expense of nutrient self-reliance outside the Okanagan. This kind of analysis should therefore be useful to explore, ideally together with food system and organic residual management actors, how different food system and organic residual management scenarios perform in terms of nutrient circularity, in the geographical area being considered, but also how it impacts nutrient flows and circularity in the places with which feed and food are traded.

Keywords: nutrient metabolism, agriculture, recycling fertilizer, nutrient recirculation, nutrient recovery, nutrient self-reliance, feed and food trade

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INTRODUCTION

The future of food is vividly debated (Garnett, 2014; Fraser et al., 2016; Willett et al., 2019). Irrespective of our food future, feeding the human population requires a continuous supply of plant nutrients for crop production. Until about a century ago, this supply relied largely on natural processes like weathering and biological nitrogen fixation, the integration of crop and livestock production, as well as the internal recycling of organic residuals,[1] such as animal manure and residues, food waste, and human excreta. But modern food systems have become highly reliant on continuous inputs of nutrients mined from finite reserves, produced using fossil fuels, and transported over large distances. The profligate input of synthetic fertilizers has compromised internal recycling of nutrients in food systems for sustained high yields (Conforti and Giampietro, 1997; Arizpe et al., 2011). Together with the globalization and specialization of agriculture, as well as urbanization, this led to nutrient flows becoming less circular (Vitousek et al., 1997; Smil, 2000; Gruber and Galloway, 2008; Nesme et al., 2018; Harder et al., 2020). In fact, the combination of contemporary diets, agricultural, and residual management practices means that a significant share of nutrient inputs is lost from agriculture and other parts of society to the atmosphere, water bodies, landfills, and so forth. Taking phosphorus as an example, globally, losses to the built and natural environment amount to around 65% of nutrient inputs to agricultural production (Elser, 2012; Cordell and White, 2014). Widespread nutrient losses severely compromise water quality (Steffen et al., 2015) and soil health (Jones et al., 2013). At the same time, the need to continuously produce new synthetic fertilizers to maintain agricultural productivity, and the fact that the production of fertilizers largely relies on mining of geological resources and is energy intensive, raises issues in terms of nutrient security (Cordell et al., 2009; Manning, 2015; Razon, 2018), particularly in some regions of the world (Jones et al., 2013). Nutrient insecurity has direct implications for our ability to meet the second Sustainable Development Goal (SDG 2), Zero Hunger. Nutrients are key productive inputs and comprehensive nutrient recycling from organic residuals can promote equal access to nutrients and enhance soil health.

Mitigating nutrient pollution in water bodies and securing future nutrient supplies requires a radical rethinking of various aspects of nutrient management and in all parts of society, from agriculture and food processing to food consumers and residual management, to reduce nutrient demand and losses, and achieve a more circular use of these essential plant nutrients (Sutton et al., 2013; McConville et al., 2015; Withers et al., 2020). It is in this light that recent years have seen significant interest in concepts like "circular nutrient solutions", "closing the nutrient loop", "nutrient circularity", and "circular nutrient economy" (Nesme and Withers, 2016; Cobo et al., 2019; Robles et al., 2020; Rosemarin et al., 2020; van der Wiel et al., 2020; Zhao et al., 2020). Given the popularity of the concept of "circular bioeconomy" in research and policy discussions, an increased demand for biomass can be expected in the years to come. The bioeconomy refers to economic activity that involves the use of biotechnology and biomass to produce energy, goods, and services. A more ecological management of nutrients and carbon through their recovery and reuse will play a central role in making the bioeconomy circular, as it enables the continued production of new crop plant biomass for food, fiber, oils, and other purposes.

As compelling as the concept of nutrient circularity is in theory, moving toward a more circular use of nutrients in practice is not trivial and is hampered by a number of factors (Barquet et al., 2020). Theoretically, achieving more circular nutrient flows would require that nutrients in organic residuals are sent back to where they came from. Obviously, it is not reasonable to expect that post-consumption of feed and food, residual nutrients go back to exactly where the feed and food were produced. But it seems reasonable to assume that, at the very least, a more circular use of nutrients would require that, in places where more feed and food are consumed than produced (e.g., urban areas or areas with intensive livestock production), nutrients available in organic residuals are redistributed to places where feed and food production exceeds consumption (e.g., rural agricultural areas or areas with predominantly crop production).

Nutrient supply and demand imbalances at larger scales, between regions with net imports or exports of feed and food, are rather difficult to balance. This is due to longer transport distances and because the coexistence of nutrient deficits and surpluses may be concealed if they occur distant from one another. The cost of utilizing nutrients in organic residuals increases with the distance the residuals have to be hauled, or with the technical processes needed to extract and concentrate nutrients so that they can be transported more easily. Therefore, it is often less costly and easier to forego utilizing nutrients in organic residuals and instead apply synthetic fertilizers to crops. Nutrient supply and demand imbalances at smaller scales, for instance between crop and livestock farms that are located in close proximity to one another, should in principle be relatively easier to balance. This is due to the shorter transport distances and because the coexistence of nutrient deficits and surpluses is more apparent if they occur in close proximity within the same geographical area. However, both at larger and smaller scales, stoichiometry of plants, and soil chemistry may complicate matters. For instance, the application of animal manures or composts to adjust soil fertility for one plant nutrient may lead to an excess or deficiency for other nutrient elements (Maltais-Landry et al., 2019).

When studying possible trajectories toward a more circular use of nutrients in modern food and bioeconomy systems, it is important to start with an analysis of nutrient flows carried out at appropriately useful scales. It has been proffered that the "local", "territorial", or "bioregional" scale, chosen to include similar political, social, and ecological characteristics, is meaningful to restore nutrient circularity (van der Wiel et al., 2020) and to study transitions toward more sustainable food and bioeconomy systems (Harris et al., 2016; Lamine et al., 2019; Wohlfahrt et al., 2019). The idea is that such scales are large enough to include a diversity of ecological and technical processes, yet small enough for various stakeholders—who may have divergent views of the challenge and how to solve it—to engage in constructive dialogue that leads to action. Regarding nutrient circularity, however, we think it would be meaningful to analyze patterns inside a given bioregion in relation to the interactions it has with its context in terms of imports and exports of nutrients.

In two previous companion papers, we introduced a novel analytical framework (Harder et al., 2021b) and calculation

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[1] While we acknowledge that the term "residue" is more commonly used in conjunction with e.g., crop or food residues, we here use the term 'residual' to be more inclusive of organic materials in e.g., municipal solid wastes and wastewater.

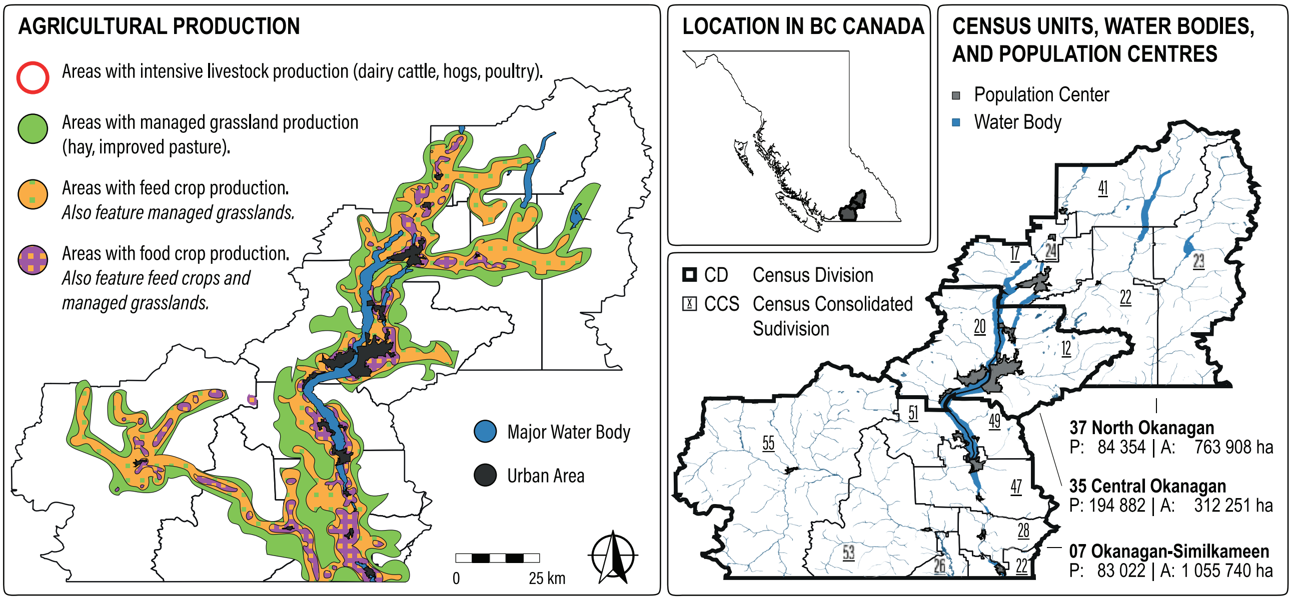

FIGURE 1 | Overview of the Okanagan bioregion. The Okanagan population is largely centered in the bioregion along the Okanagan Lake. Crop production takes place mainly on and near valley bottoms, with feed crops and managed grassland extending progressively further away. Intensive livestock production is concentrated in two areas in the north of the bioregion and coincides with areas of intensive feed production. Grazing on rangeland and natural pastures is commonplace in the foothill areas toward the periphery in the northeast and southwest of the bioregion. P = population and A = area. Figure adapted from Harder et al. (2021a).

method (Harder et al., 2021a) to assess the circularity of nutrient flows in food systems across nested scales. The key novelty of the proposed approach was that it analyzes the entanglement of nutrients flows, not only inside a bioregional food system, but also in relation to the nutrient flows that feed and food imports and exports cause outside of the spatial boundaries of the considered food system. In this paper, we expand upon our previous work by applying the methodology to evaluate a suite of food system scenarios in the Okanagan bioregion in BC Canada, for the year 2050, in terms of the flows of nitrogen (N), phosphorus (P), potassium (K), and magnesium (Mg). The over-arching objective was to explore whether this line of research is a meaningful way of evaluating food system and organic residual management scenarios from the perspective of nutrient management and the potential for a more circular use of nutrients. Specifically, we set out to compare nutrient flows and nutrient circularity in the food system and organic residual management infrastructure of the Okanagan bioregion, for a suite of food system scenarios representing the year 2050.

METHODS

The Okanagan Bioregion

The Okanagan, also known as the Okanagan Valley, is a region located in the Southern Interior of British Columbia (BC), Canada. With a population of 362,000, the Okanagan is the most populous region in the BC Interior. With a total area of just above 2 million hectares, the Okanagan is one of the two most important agricultural regions in BC, and one of the largest producers of temperate zone tree fruits, wine grapes, and wines in Canada (Robert et al., 2018). A map of the Okanagan is provided in **Figure 1**, indicating agricultural production areas, as well as major water bodies and population centers.

Scenarios

Food System

In addition to the year 2016 baseline (BAS), we considered four food system scenarios that represent the year 2050. Scenarios were chosen such that they allow examination of effects of population levels, dietary change, the composition of agricultural production, and the quantity of agricultural land in production (**Table 1**). In the business-as-usual scenario (BAU), the agricultural production system and diet regime remain unchanged, while population increases by a projected 40% relative to 2016 levels. In the basic food self-reliance scenario (FSR), agricultural production is optimized for food self-reliance, with all else as in the BAU scenario. Optimization for food self-reliance was modeled such that agricultural land in the Okanagan that currently produces crop commodities for export is re-allocated to the production of crop commodities to satisfy local food need in the Okanagan. The FSR scenario was chosen because various actors in the bioregion are actively pursuing a food system future in terms of regionalizing the food system and increasing food self-reliance. The planetary health diet scenario (EAT) represents a situation where the diet changes from a conventional to one in line with the recommendations by the EAT-Lancet commission, with all else as in the FSR scenario. The healthy reference diet recommended by the EAT-Lancet Commission largely consists of whole grains, legumes, nuts, vegetables, fruits, and unsaturated oils; it includes a moderate

TABLE 1 | Overview of the year 2016 baseline and the four food system scenarios for 2050 considered in this study.

Code	Year	Agriculture	Land base	Diet	Population	Comment
BAS	2016	Current	Current	Current	Current	Actual situation in 2016.
BAU	2050	Current	Current	Current	Increased	Increasing population.
FSR	2050	Food self-reliance	Current	Current	Increased	Optimization for food self-reliance.
EAT	2050	Food self-reliance	Current	Planetary health	Increased	Dietary change.
EXP	2050	Food self-reliance	Expanded	Planetary health	Increased	Plus 50% arable land.

amount of seafood and poultry but only little red meat, processed meat, added sugar, refined grains, and starchy vegetables (Willett et al., 2019). This diet was chosen because a diet that is low in meat but still contains some meat likely finds broader acceptance than a strictly vegetarian or vegan diet. This choice also aligns with the idea that there may be a place for livestock in future food systems, as long as it is raised on “ecological leftovers” not suitable for human consumption (Röös et al., 2016; Van Zanten et al., 2018; Karlsson and Röös, 2019). The expanded land base scenario (EXP) explores a hypothetical situation where agricultural production is expanded to all suitable land for agriculture, with all else as in the EAT scenario. This scenario could be the result of conscious efforts within the Okanagan to maximize local food supply and concomitant economic opportunities by increasing local production and realigning local demand through dietary change.

For the BAS and BAU scenarios, production of agricultural commodities in the Okanagan was estimated based on agricultural statistics representative of the baseline year. For the scenarios that are optimized for food self-reliance (i.e., FSR, EAT, EXP), the total area of agricultural land in production served as starting point. While we acknowledge that the production mix could be changed in many ways to increase food self-reliance, for the purpose of this analysis, we assumed that the structure of agricultural production is subject to some inertia and thus would include elements from the baseline. To this effect, we first capped local production of individual food commodities so that they would not exceed local consumption demand. Then, we proportionally increased the production areas of individual crop commodities until the total production area reached the total area of agricultural land in production as per the scenario specification. In doing so, the production of individual crop commodities was not increased beyond what is needed to fully supply local demand. Of note, expansion of agriculture in the EXP scenario was applied only to arable land but not to rangeland and not to livestock numbers in the bioregion.

Organic Residual Management

In the year 2016, municipal wastewater treatment was available for the larger and some smaller communities, amounting to overall coverage of about 60%. The remaining 40% of the population utilized onsite sanitation systems. Municipal solid waste management did not provide for separate collection of food waste—unless composted at home or taken care of by collection schemes other than the municipal ones, food waste thus mostly ended up on landfills as part of mixed household waste. In a similar vein, it appeared that nutrients in animal residues such as slaughterhouse waste were not recovered. Regarding animal manure, it was difficult to know what portion was effectively returned to crop production—there was neither centralized infrastructure for manure management, nor reliable statistics. We assumed that manure was generally adequately managed but transport over larger distances was limited. Estimated nutrient recovery efficiencies for the baseline year 2016 are summarized in **Table 2**. In addition to the year 2016 baseline recovery efficiencies, we considered a situation that reflects a long-term potential for nutrient recovery from organic residuals. For instance, separate collection of food waste is being planned. To represent the long-term potential for nutrient circularity, we did not delineate a specific future organic residual management infrastructure. Rather, we assumed that nutrient recovery rates could be increased to 70% for all nutrients and across all types of organic residuals. This reflects an ambitious estimate of the recovery rates that full-scale recovery technologies can be realistically expected to achieve.

Assessing Nutrient Circularity

The conceptual framework that underpinned our analysis is presented in detail in a companion paper (Harder et al., 2021b). The implementation of the calculation model is described in detail in a second companion paper (Harder et al., 2021a). Here, we provide a brief summary of the core features of the analytical framework and calculation model.

Structure of the Analysis

The analysis encompassed five subsystems: (i) agricultural land; (ii) livestock production; (iii) food processing; (iv) food consumption, and (v) residual management. Because of feed and food imports and exports, the spatial extent of these subsystems transcends the boundaries of the Okanagan bioregion. For example, Okanagan livestock may eat imported feed. Likewise, feed and food exported from the Okanagan gives raise to the generation of organic residuals outside of the bioregion. To this effect, as conveyed in **Figure 2**, our analysis distinguished between subsystem components considered internal to the Okanagan (i.e., that lie inside the spatial boundaries of the bioregion) and subsystem components considered external to the Okanagan (i.e., that lie outside the spatial boundaries of the bioregion). In other words, functionally, our analysis included all nutrient flows that relate to food production and consumption in the Okanagan. Spatially, we distinguished an internal component that represents the bioregional food system in the Okanagan, and

TABLE 2 | Recovery and reuse ratios for various organic residuals, for the year 2016 baseline and one scenario for 2050 that represents a realistic recovery potential.

Code	Waste management	Type of organic residual	Basis for estimation	N	P	K	Mg
CUR	Baseline	Animal manure	Educated guess	0.40	0.60	0.60	0.60
		Animal residues	Waste management infrastructure	0.00	0.00	0.00	0.00
		Food waste	Waste management infrastructure	0.00	0.00	0.00	0.00
		Human excreta	Waste management infrastructure	0.35	0.66	0.17	0.17
POT	Realistic potential	All types of organic residuals	Recovery technology performance	0.70	0.70	0.70	0.70

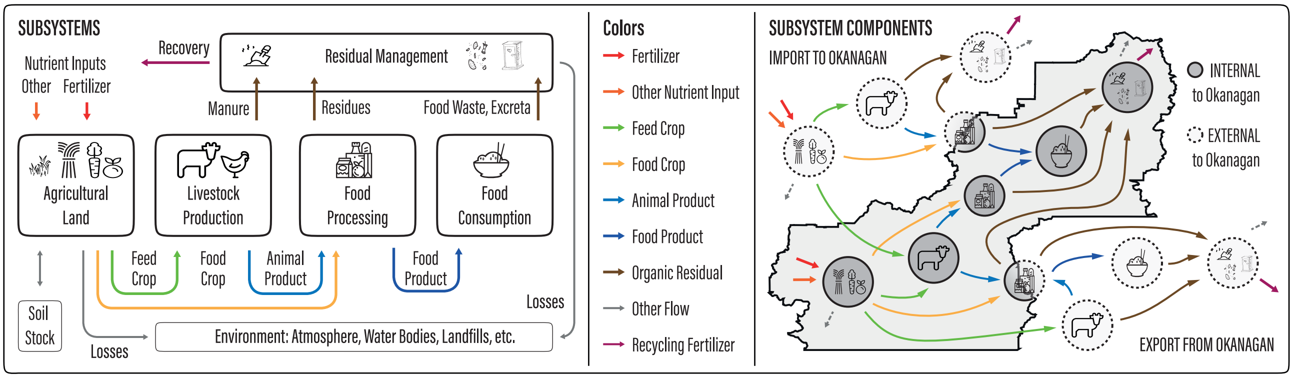

FIGURE 2 | Structure of the analysis. Functionally, the analysis encompasses five subsystems that are connected to one another as shown in the left part of the figure. For each subsystem, spatially, the analysis distinguishes one component internal and one external to the Okanagan, which is shown in the right part of the figure. Note that, for clarity, the external component is split into two parts: one relates to imports into and one to exports from the Okanagan. Figure adapted from Harder et al. (2021a).

an external component that represents that part of the global food system with which the bioregional food system interacts through imports and exports of feed and food. Of note, the external component was not further specified in terms of its spatial location other than that it is outside the spatial boundaries of the Okanagan.

Nutrient Circularity Indicators

Our objective was to assess nutrient circularity not only inside the Okanagan, but also how trade impacts nutrient circularity in the areas from and to which the Okanagan imports and exports feed and food. This required a more detailed understanding of nutrient circularity and its relationship with system openness, as explained in **Figure 3**.

Nutrient circularity is generally conceived of as some sort of comparison between nutrient inputs to biomass production (in terms of fertilizer inputs only, or considering nutrient inputs more broadly) and nutrients in organic residuals (in terms of what is actually recirculated, or considering what is potentially available) (e.g., Senthilkumar et al., 2014; Metson et al., 2016; Parchomenko and Borsky, 2018; Trimmer and Guest, 2018; Akram et al., 2019; Leinonen et al., 2019). This comparison can focus on inputs (i.e., "self-reliance" in terms of the share crop removal that can be supplied with recirculated nutrients) or on outputs (i.e., "recycling rate" in terms of the share of nutrients in organic residuals that are recirculated) (top part of **Figure 3**). Moreover, as our analysis expanded beyond the spatial boundaries of the Okanagan, it was possible to distinguish internal and external self-reliance and internal and external recycling rate.

The internal and external recycling rate depends entirely on the respective residual management infrastructure within and outside the Okanagan. The internal and external self-reliance is determined not only by the structure and location of residual management but also by the structure and location of agricultural production and the extent of agricultural trade. Therefore, internal and external self-reliance are unlikely to be at the same level. Feed and food imports to the Okanagan, for instance, will contribute to a higher nutrient self-reliance internal to the Okanagan but a lower nutrient self-reliance external to the Okanagan. This is because nutrient inputs to agricultural production outside the Okanagan boost the source of nutrients in residuals within the Okanagan. *Vice versa*, feed and food exports from the Okanagan will contribute to a lower nutrient self-reliance internal to the Okanagan but a higher nutrient self-reliance external to the Okanagan. This is because nutrient inputs to agricultural production within the Okanagan boost the source of nutrients in residuals outside the Okanagan. To assess the degree to which consumption and trade of feed and food move nutrients from agricultural land in one place to organic residuals in another place, we also evaluated what we refer to as system openness (bottom part of **Figure 3**).

System openness can lead to what we refer to as nutrient depletion or accumulation—imbalances in nutrient need and availability that are the result of imbalances in feed and food

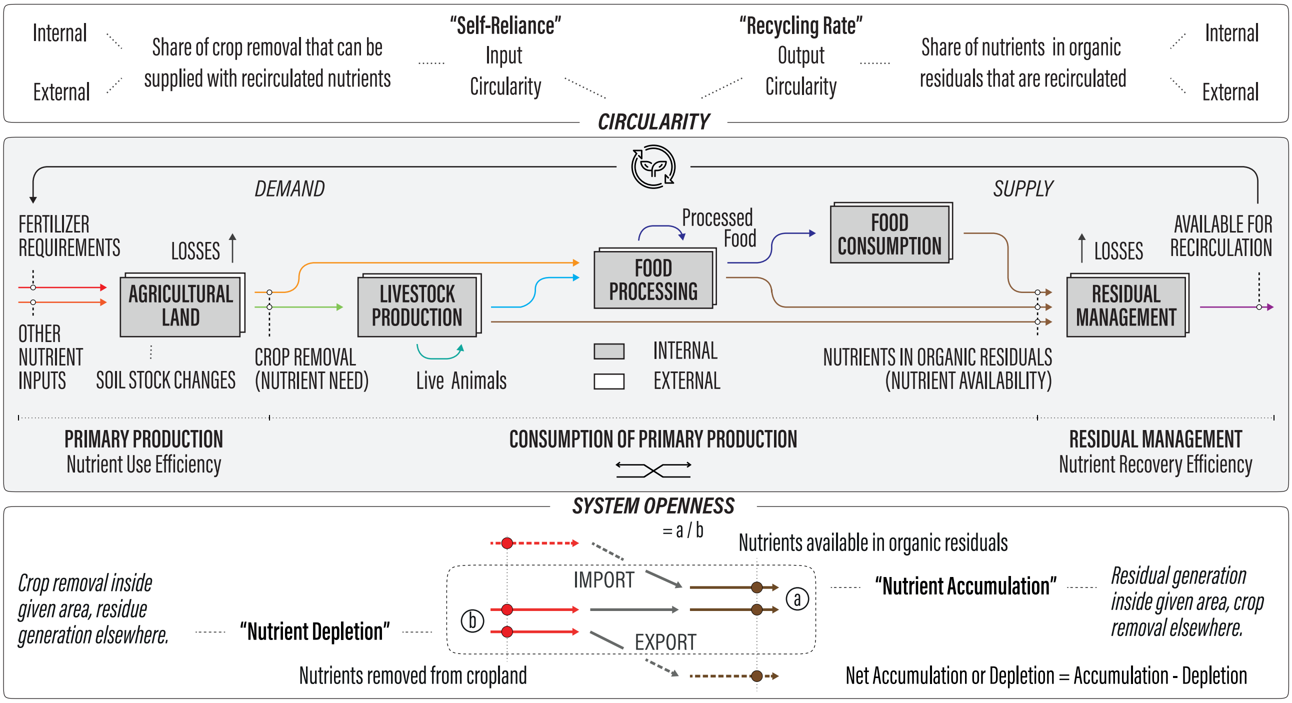

FIGURE 3 | Detailed analysis of the relationship between nutrient circularity and system openness. The middle part of the figure shows nutrient flows between the five subsystems. The top part of the figure distinguishes two notions of nutrient circularity, one focusing on outputs from residual management (recycling rate) and one on inputs to agricultural production (self-reliance). Both self-reliance and recycling rate can be estimated separately internal and external to the Okanagan. System openness is explained in the bottom part of the figure. The idea is that import of agricultural commodities leads to "nutrient accumulation" in the bioregion whereas the opposite holds true for export. System openness for a given nutrient element was defined as the proportion of this nutrient element in the harvest in the bioregion (b) that is available in organic residual in the bioregion (a). If a/b > 1, the bioregion benefits from nutrient inputs elsewhere. If a/b < 1, the opposite holds true. Figure adapted from Harder et al. (2021a,b).

imports and exports. The idea behind the concept of nutrient accumulation and depletion, as proffered herein, is that nutrients available in organic residuals are tracked back to the places nutrient inputs to crop production were applied (i.e., inside or outside the bioregion). In this way, it is possible to elucidate how much the Okanagan benefits from nutrient inputs elsewhere, and *vice versa*. Net nutrient accumulation or depletion (accumulation less depletion) represents the difference between nutrients in organic residuals and crop removal, internal or external to the Okanagan. Estimating system openness internal and external to the Okanagan separately helps quantify the extent to which potential imbalances in feed and food trade contribute to nutrient accumulation or depletion both internal and external to the Okanagan.

It is worthwhile to note that, in our conceptual model, there are no losses in the subsystems livestock production, food processing, and food consumption. Any losses not inherent in grass and crop production take place in residual management. For example, for cows in a livestock operation this means that residual management starts upon manure excretion. Likewise, losses during housing are considered as losses during residual management. Therefore, in the absence of feed and food trade, or in case of balanced trade, nutrients removed with the harvest in the Okanagan would equal nutrients available in organic residuals in the Okanagan. The larger the discrepancy between "crop removal" and "nutrients in organic residuals" in the middle part of **Figure 3**, the more open the system is. Note that system openness does not say anything about the leakiness of the system in terms of nutrient losses to for instance landfills and water bodies. System openness simply indicates the extent to which nutrient inputs in one place become available in residuals in another place. Losses can occur both in agricultural production and in residual management and are taken into account in the recycling rate and the self-reliance indicators.

Calculation Model

In summary, the calculation model that underpinned our analysis maps the relationships between nutrient inputs and outputs for each of the five subsystems considered. As conveyed in **Figure 4**, the first calculation step consisted of estimating commodity flows, both in terms of the production of agricultural commodities and the consumption of food commodities in the Okanagan and in terms of imports and exports. Imports and exports were estimated based on a suite of allocation principles and assumptions given that there were no import and export statistics for the Okanagan. Note that, even though it is known that seasonality constraints imply that domestic production may not actually supply domestic demand (see Dorward et al., 2017),

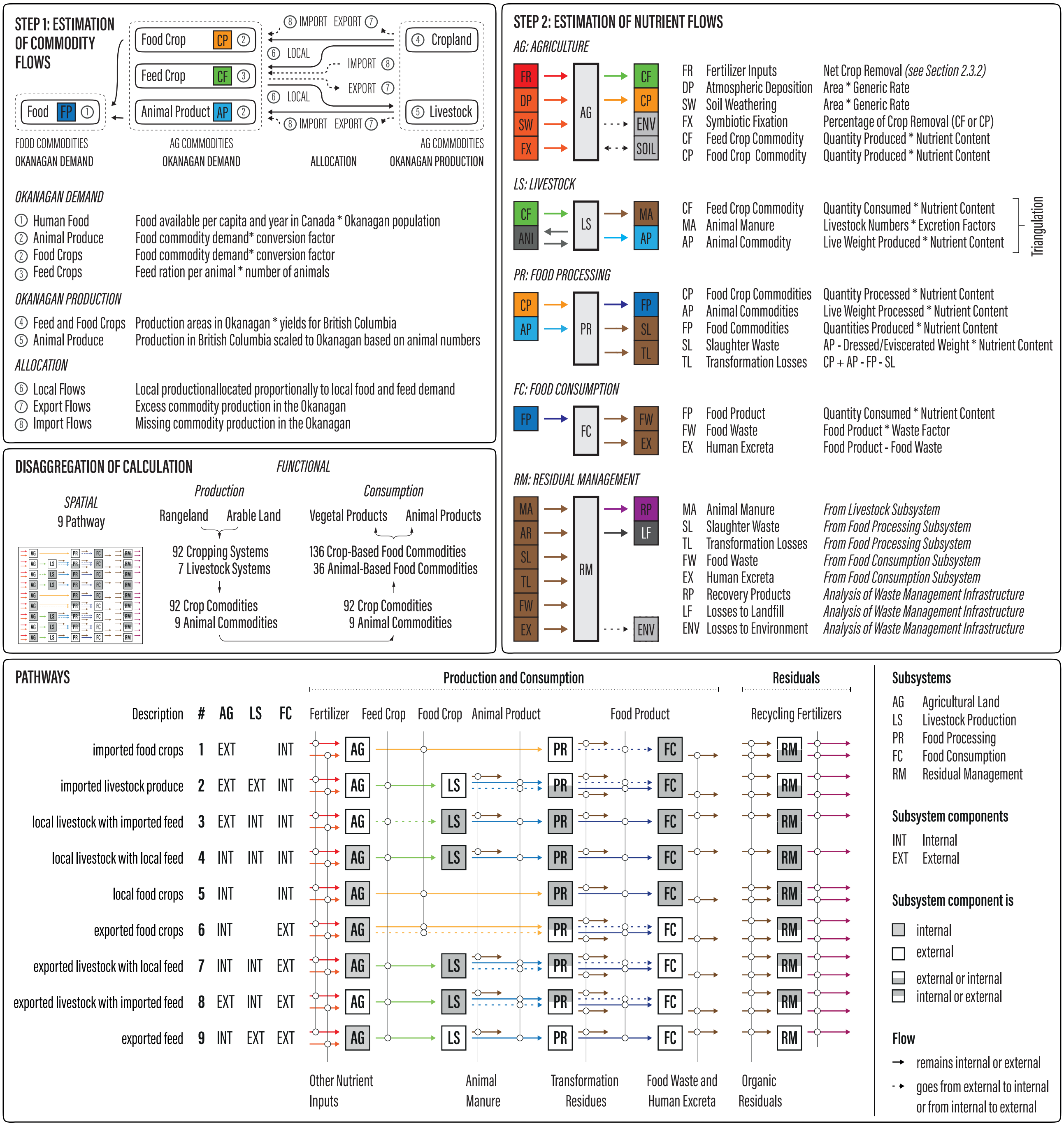

FIGURE 4 | Procedure for estimating nutrient flows. The first step was to estimate commodity flows. The second step was to translate commodity flows into nutrient flows. Calculations were carried out separately per commodity and for nine pathways from crop production to food consumption (see "disaggregation of calculation"). Each pathway describes a unique combination of where the crop and livestock commodities are produced, and the food commodities are consumed (see "pathways"). The idea with these separate pathways was to be able to track nutrients nutrients from crop production to organic residual generation as a function of whether certain subsystem components are internal or external to the Okanagan. Figure adapted from Harder et al. (2021a).

the calculations did not account for this. Unlike in the case of food self-reliance, from the point of view of nutrient circularity, it does not matter if, for example, apples are imported in spring and the same amount is exported in fall (assuming that their nutrient content is similar). The second calculation step consisted of estimating nutrient flows, making sure that the origin of nutrients is properly accounted. To this end, the conceptual model and calculation approach were implemented such that the

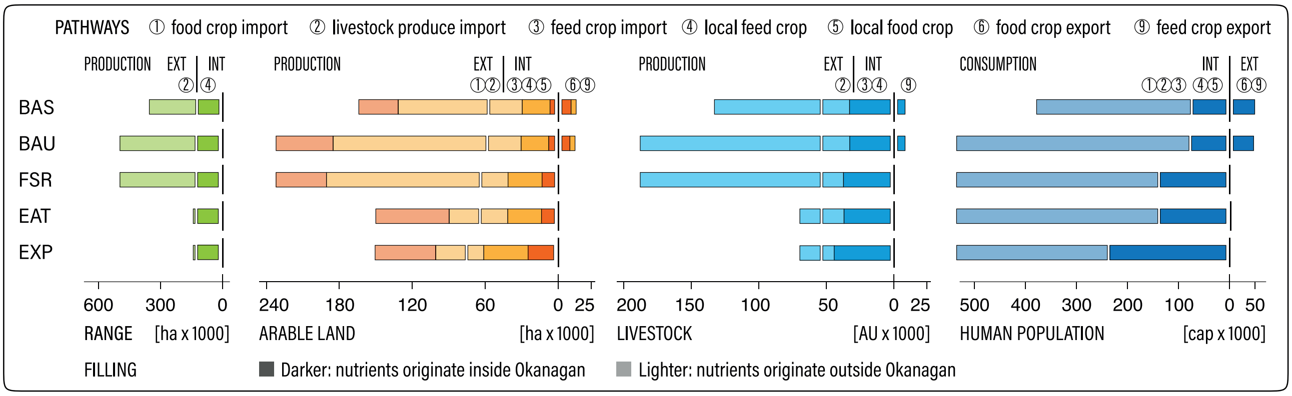

FIGURE 5 | Production of agricultural commodities and consumption of food commodities across food system scenarios. Circled numbers at the top of the figure refer to pathways as per **Figure 4**.

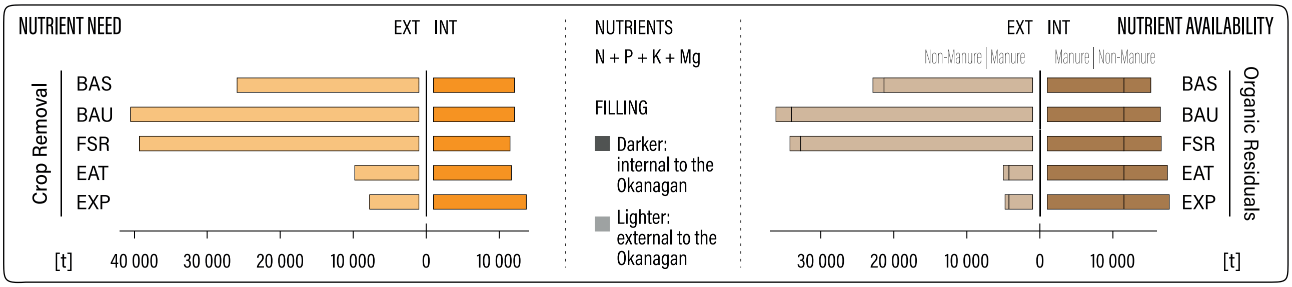

FIGURE 6 | Nutrient need (crop nutrient removal) and nutrient availability (nutrients in organic residuals) across food system scenarios. Note that the numbers for all four considered nutrient elements were added together.

key model outputs are separate nutrient flows between subsystem components for the nine pathways shown in **Figure 4**.

RESULTS

Results for the year 2016 baseline are reported in detail in a companion paper (Harder et al., 2021a). Here, we focus on the four scenarios for the year 2050.

Commodity and Nutrient Flows Across Scenarios

Population Increase

Population increase (BAS to BAU) has a minimal effect on agricultural production in the Okanagan (**Figure 5**). Slightly fewer food crops are exported and instead go to local consumption, which can be seen in the slight shift from pathway 6 (exported food crops) to pathway 5 (local food crops). The majority of the additional demand is supplied by imports. This can be seen in a significant increase in pathway 1 (imported food crops) and pathway 2 (imported livestock produce). Consequently, as shown in **Figure 6**, crop nutrient removal increases external to the Okanagan, as this is where the additional commodities needed to meet the additional demand are mostly produced. The total quantity of nutrients in organic residuals that would be available for recovery increases both internal and external to the Okanagan—internally mostly because of an increased generation of food waste and human excreta and externally mostly because of an increased generation of animal manure that results from higher imports of livestock products. As shown in **Figure 7**, nutrient accumulation for manure residuals does not increase, because the number of animals in the Okanagan and the source of their feed do not change as per our scenario definition. Nutrient accumulation for non-manure residuals increases due to the increase in food consumption in the Okanagan. Taken together, this means an increased net nutrient accumulation in the Okanagan.

Food Self-Reliance

Optimization for food self-reliance (BAU to FSR) means that the Okanagan no longer exports agricultural commodities and that all of the food produced in the Okanagan is consumed locally (**Figure 5**). Given that export from the Okanagan is smaller than production for local supply and import, crop nutrient removal both internal, and external to the Okanagan remain virtually unchanged (**Figure 6**). Manure generation internal to the Okanagan does not change as animal numbers remain the same. Manure generation external to the Okanagan decreases slightly as there is no more feed export from the

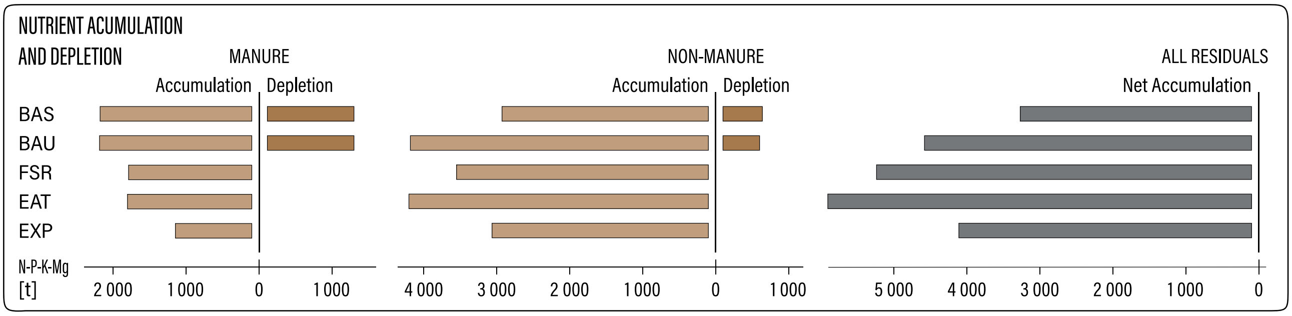

FIGURE 7 | Nutrient accumulation and depletion across food system scenarios. Note that the numbers for all four considered nutrient elements were added together.

Okanagan. For both manure and non-manure residuals, nutrient accumulation in the Okanagan decreases and there no longer is nutrient depletion (**Figure 7**). This mirrors the ceasing of exports and consequently a larger share of food consumption in the Okanagan now comes from local consumption. Taken together, net nutrient accumulation is somewhat increased.

Dietary Change

Dietary change toward a planetary health diet (FSR to EAT) reduces the consumption of animal products and increases consumption of plant-based products. The reduced demand for animal products means that more land is required for food crop production and less for feed crop production. Internal to the Okanagan, there are no changes to agricultural production (**Figure 5**). This is because even the reduced demand of livestock still exceeds local production. But external to the Okanagan, there is a significant reduction in livestock numbers, as much fewer animal products need to be imported. As a consequence, there is also much less land needed outside the Okanagan to grow feed, see pathway 2. At the same time, the increased demand for food crop products means that imports increase, see pathway 1. Crop nutrient removal internal to the Okanagan is not affected appreciably, but there is a pronounced effect in regard to reducing crop nutrient removal external to the Okanagan (**Figure 6**). Nutrients available in animal manure are drastically reduced, most notably external to the Okanagan. This is because fewer animal products are consumed, which significantly reduces imports of animal products. For nutrients available in non-manure residuals, the effect of dietary change is minimal. Nutrient accumulation related to animal manure does not change as changes to livestock numbers take place external to the Okanagan. There is a slight increase in nutrient accumulation related to non-manure residuals, as well as to net nutrient accumulation.

Expansion of Agricultural Land in Production

Land base expansion (EAT to EXP) was modeled such that it affects only crop production while livestock production does not increase. Given that population and diet do not change, total land use—internal plus external to the Okanagan—remains constant (**Figure 5**). Expansion of agricultural production simply means that a higher share of the food commodities consumed in the Okanagan comes from local production, so that a lower share needs to be imported. Consequently, overall total nutrient need does not change either—it simply increases internal to the Okanagan and commensurately decreases external to the Okanagan. Similarly, the overall availability of nutrients in organic residuals slightly increases in the Okanagan and commensurately decreases external to the Okanagan. This is because increased local supply also means increased local food processing, which shifts some of the associated nutrient losses from external to internal to the Okanagan. All in all, nutrient accumulation both related to animal manure and non-manure residuals, as well as net nutrient accumulation decrease. This is because local production responds directly to expansion of agriculture land while consumption in the Okanagan remains constant.

Nutrient Circularity Across Scenarios

System Openness

System openness across food system scenarios is shown in **Table 3**, which clearly reveals that net feed and food imports to the Okanagan lead to an increased quantities of nutrients in organic residuals across all scenarios considered. At the same time, it becomes very apparent that this comes at the expense of reducing quantities external to the Okanagan. Note that the significantly smaller numbers for system openness external to the Okanagan for the EAT and EXP scenarios are the result of overall smaller nutrient flows external to the Okanagan upon dietary change from a conventional to the planetary health diet. In absolute terms, the Okanagan benefits from nutrient inputs elsewhere under these dietary change and land expansion scenarios in a way similar to the BAU and FSR scenarios. But in relative terms, this impact becomes more pronounced when overall nutrient flows external to the Okanagan are smaller, as under EAT and EXP. Another pattern that is noteworthy is that system openness is larger for nitrogen and phosphorus than for potassium and magnesium. This reflects that in livestock production, relatively more nitrogen and phosphorus partition into the livestock product rather than manure as compared to potassium and magnesium.

Nutrient Self-Reliance

To assess nutrient self-reliance for current residual management practices and the long-term potential, crop nutrient removal was contrasted with nutrients recovered per current recovery

TABLE 3 | System openness across scenarios, internal and external to the Okanagan.

	Internal				External			
Scenario	**N**	**P**	**K**	**Mg**	**N**	**P**	**K**	**Mg**
BAS	1.49	1.56	1.02	1.22	0.81	0.80	0.99	0.90
BAU	1.67	1.75	1.07	1.30	0.83	0.83	0.98	0.91
FSR	1.70	1.73	1.21	1.39	0.82	0.82	0.94	0.89
EAT	1.78	1.77	1.23	1.50	0.41	0.41	0.59	0.46
EXP	1.43	1.37	1.15	1.26	0.51	0.52	0.68	0.56

Numbers larger than 1 indicate a net nutrient accumulation, numbers smaller than 1 a net nutrient depletion as a result of feed and food trade.

TABLE 4 | Nutrient self-reliance—current residual management practices.

	Internal				External			
Scenario	**N**	**P**	**K**	**Mg**	**N**	**P**	**K**	**Mg**
BAS	0.49	0.72	0.54	0.63	0.30	0.41	0.57	0.51
BAU	0.53	0.79	0.54	0.63	0.31	0.43	0.57	0.53
FSR	0.53	0.77	0.62	0.67	0.31	0.43	0.56	0.52
EAT	0.56	0.82	0.61	0.67	0.13	0.17	0.31	0.23
EXP	0.44	0.62	0.57	0.55	0.17	0.23	0.37	0.30

Numbers larger than 1 indicate a nutrient surplus, numbers smaller than 1 a nutrient deficit.

efficiencies. For the purpose of this analysis, it was simply assumed that fertilizer requirements equal crop nutrient removal. In reality, depending on the extent of nutrient losses and inputs through other sources, fertilizer requirements may be larger or smaller than crop nutrient removal. Nutrient self-reliance can thus be improved by increased agronomic efficiency and greater reliance on biological nitrogen fixation.

For all nutrients considered, there are greater quantities in animal manure than in other organic residuals, both internal and external to the Okanagan. This pattern does not change across scenarios. With current residual management practices, across all scenarios, nutrients recovered from organic residuals are insufficient to meet crop nutrient needs, both internal and external to the Okanagan (**Table 4**).

With improved nutrient recovery, across all scenarios, it should be possible to meet nitrogen and phosphorus needs (i.e., compensate for crop removal) internal to the Okanagan, but this does mostly not apply to potassium and magnesium (**Table 5**). External to the Okanagan, across all scenarios and nutrients, recovered nutrients are still insufficient to meet nutrient need.

DISCUSSION AND OUTLOOK

A number of recent studies have assessed the potential of nutrients in organic residuals to supply the nutrient inputs required for crop production (e.g., Metson et al., 2016; Parchomenko and Borsky, 2018; Trimmer and Guest, 2018; Akram et al., 2019; Leinonen et al., 2019). These studies concerned larger areas than the Okanagan, and for the most part featured a higher spatial resolution. Our analysis differed from previous studies in that it assessed not only nutrient circularity internal to a given geographical area, but also how feed and food trade influence nutrient circularity external to it. To this effect, we applied an innovative accounting scheme for nutrient flow analysis in food systems utilizing a suite of food system scenarios in the Okanagan bioregion in British Columbia, Canada. In this way, it was possible to explore, in quantitative terms, the impact of feed and food trade on nutrient circularity. This kind of analysis should be useful to explore, ideally together with food system and organic residual management actors, how different food system and organic residual management scenarios impact nutrient circularity, locally in the geographical area being considered, but also in the places with which feed and food are traded.

TABLE 5 | Nutrient self-reliance—long-term potential.

	Internal				External			
Scenario	**N**	**P**	**K**	**Mg**	**N**	**P**	**K**	**Mg**
BAS	1.05	1.09	0.71	0.86	0.57	0.56	0.69	0.63
BAU	1.17	1.22	0.75	0.91	0.58	0.58	0.69	0.64
FSR	1.19	1.21	0.85	0.98	0.58	0.57	0.66	0.62
EAT	1.25	1.24	0.86	1.05	0.29	0.29	0.42	0.32
EXP	1.00	0.96	0.81	0.88	0.36	0.36	0.47	0.39

Numbers larger than 1 indicate a nutrient surplus, numbers smaller than 1 a nutrient deficit.

Key Findings

While it was possible to discern differences across scenarios internal to the Okanagan, differences often were more pronounced external to the Okanagan, notably in response to population increase and diet change. Our analysis also clearly revealed the extent to which improvements in nutrient self-reliance in the Okanagan affect nutrient self-reliance external to the Okanagan, in the areas with which feed and food are traded. These findings further emphasize the importance of considering circularity across nested scales (see also Koppelmäki et al., 2021). To be clear, a lowered nutrient self-reliance external to the Okanagan does not imply that nutrient self-reliance in the places with which the Okanagan trades feed and food in absolute terms needs to be lower than in the Okanagan. This depends on the extent to which these external regions import and export feed and food with other regions outside the Okanagan. Rather, what our analysis shows is that, overall, the Okanagan lowers nutrient self-reliance outside its spatial boundaries in comparison to a hypothetical situation where feed and food trade with the Okanagan were in balance.

As for the Okanagan, if nutrient circularity was strived for, the best strategy would be to utilize all suitable arable land in the bioregion and shift toward a more plant-based diet (scenario EXP). But even with these measures in place, more than half of the food consumed would originate in feed or food crops produced outside the bioregion. Even if population growth in the bioregion was restricted, this number would not go lower than about one third at best. In light of the net nutrient accumulation in the Okanagan, which takes place irrespective of the food system scenario, there is a clear need for comprehensive nutrient recovery from organic residuals, including food waste and human excreta. Moreover, part of the recovered nutrients ought to be made available to places outside the Okanagan to compensate for nutrient imports with feed and food. In other words, in the face of system openness due to feed and food trade, nutrient recovery in the bioregion should exceed that needed for supplying local nutrient needs.

Potential Limitations and Desirable Model Refinements

Our approach, which involved the modeling of both the food and organic residual management system, was quite data intensive. For some aspects of the model, however, there were no reliable data. This applied in particular to the fate of nutrients in animal manures and residues, where quite coarse assumptions were applied. Likewise, calculations for the various subsystems followed a rather rudimentary approach. For example, we modeled livestock systems as a black box based on data available in agricultural statistics rather than taking a process-based approach. Also, the technical coefficients (crop yields, characteristics of livestock systems, structure and performance of organic residual management, etc.) external to the Okanagan were assumed to be the same as internal to the Okanagan. We considered these simplifications a good enough approximation for the purpose of this assessment.

Still, in light of other recent method development in the field of nutrient flow analysis, there undoubtedly is ample room for refining our approach by integrating some of the work done by other researchers in the field. One addition that would be particularly valuable is to compare not only the quantities of nutrients that are required for crop production and available in residuals, but also what form they are in and whether that implies certain constraints given a certain agronomic context (see Trimmer et al., 2019). To this effect, it would be important to also consider the stoichiometry of soil and crop nutrient demand, including carbon. If the stoichiometry of a recycled fertilizer product does not match soil or crop needs, this either leads to over fertilization with some nutrients, or that some nutrients need to be replenished from other sources (Nelson and Janke, 2007; Maltais-Landry et al., 2016). In this regard, it would be particularly illustrative to investigate the potential contributions of increased agronomic nutrient use efficiency and better integration of biological nitrogen fixation into agricultural production systems. It would also be sensible to further disaggregate the analysis so that it separately considers for instance rangeland and arable land, or even different farming practices on arable land insofar as they differ in terms of nutrient use efficiency and biological nitrogen fixation. This is because it can be expected that, without improved microbially mediated nutrient use efficiency and the increased integration of biological nitrogen fixation, nutrient recovery from organic residuals will not be sufficient to fully overcome the reliance on industrial fixation or mining of nutrients.

Future Work

At this juncture, our analysis can be regarded as a proof-of-concept illustrated with a case study. In the future, we would welcome more case studies like the one presented here. If this type of approach wants to gain traction to inform policy, it would be important to conduct a thorough sensitivity and uncertainty analysis. This would benefit from implementing the calculation model in a programming language like Julia or R. Moreover, to explore scenarios beyond the status quo in production, supply, and residual management, it would be helpful to expand the model so that it allows to consider how changes at the level of individual production systems (e.g., from conventional production to organic production, or from annual to perennial systems) would affect nutrient circularity. This would allow actors in different sectors better understand their role and impact. Finally, it would be desirable to embed future case studies in a co-production approach. That is, the model would be run by a research team to help a broader group of societal actors explore the implications and plausibility of different food system and organic residual management scenarios across nested spatial scales. Such an approach would follow current best practice in sustainability assessment in that it would fully embrace the increasing understanding that co-production by academics and non-academics promises to better address the complex nature of contemporary sustainability challenges than more traditional scientific approaches (Zijp et al., 2016; Matthews et al., 2019; Norström et al., 2020). Either way, our work demonstrates the importance of explicitly considering the entanglement of nutrient circularity across scales, locally in the food system being considered, as well as in the places with which feed and food are traded.

DATA AVAILABILITY STATEMENT

A description of data sources along with model input data and calculation outputs can be found in the **Supplementary Material**. Requests to access raw data should be directed to Robin Harder, robin.harder@wetryharder.ch.

AUTHOR CONTRIBUTIONS

RH: conceptualization, methodology, software, formal analysis, investigation, data curation, writing—original draft, visualization, project administration, and funding acquisition (analysis of nutrient circularity). KM: conceptualization, writing—review and editing, project administration, and funding acquisition (Okanagan Bioregion Food System Project). SS: conceptualization, writing—review and editing, and supervision. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.661870/full#supplementary-material

Supplementary Material 1 | Calculation methodology in detail.

Supplementary Material 2 | Spreadsheet model used for calculations.

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SYSTEMATIC REVIEW
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Crop Domestication, Root Trait Syndromes, and Soil Nutrient Acquisition in Organic Agroecosystems: A Systematic Review

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Selecting crops that express certain reproductive, leaf, and root traits has formed detectable, albeit diverse, crop domestication syndromes. However, scientific and informal on-farm research has primarily focused on understanding and managing linkages between only certain domestication traits and yield. There is strong evidence suggesting that functional traits can be used to hypothesize and detect trade-offs, constraints, and synergies among crop yield and other aspects of crop biology and agroecosystem function. Comparisons in the functional traits of crops vs. wild plants has emerged as a critical avenue that has helped inform a better understanding of how plant domestication has reshaped relationships among yield and traits. For instance, recent research has shown domestication has led important economic crops to express extreme functional trait values among plants globally, with potentially major implications for yield stability, nutrient acquisition strategies, and the success of ecological nutrient management. Here, we present an evidence synthesis of domestication effects on crop root functional traits, and their hypothesized impact on nutrient acquisition strategies in organic and low input agroecosystems. Drawing on global trait databases and published datasets, we show detectable shifts in root trait strategies with domestication. Relationships between domestication syndromes in root traits and nutrient acquisition strategies in low input systems underscores the need for a shift in breeding paradigms for organic agriculture. This is increasingly important given efforts to achieve Sustainable Development Goal (SDG) targets of Zero Hunger via resilient agriculture practices such as ecological nutrient management and maintenance of genetic diversity.

Keywords: agroecology, breeding, ecological nutrient management, food security, functional traits, wild relatives, sustainable development goals

INTRODUCTION

Transformations Toward Resilient Agroecosystems

There has been considerable expansion in research focused on better understanding viable pathways toward sustainable agricultural systems, from ecological intensification to diversified farming systems and agroecological practices (DeLonge et al., 2016). Many scholars and scientists believe we are currently in a watershed moment for transformation in agricultural practices, which are paralleled by efforts to achieve Sustainable Development Goal (SDG) targets of Zero Hunger through resilient agriculture practices, enhanced on-farm diversity, and maintenance of genetic diversity (Blesh et al., 2019). Within this context, a shift from inorganic inputs to organic amendments has been a central focus for addressing many of our pressing agricultural issues (Chen et al., 2018; Isaac et al., 2018). While organic transformations are key for ensuring sustainable food production landscapes into the future, such transitions require (1) well-developed diagnostics of the plant-soil continuum under organic amendments, and (2) a better understanding of the role crop genetic resources play in governing soil nutrient management and crop acquisition strategies.

Soil Amendments, Nutrient Availability, and Crop Performance

Most modern crop species and genotypes are adapted to exploit nutrient-rich habitats through traits that confer fast growth and rapid rates of nutrient uptake (Lambers and Poorter, 1992). However, as most artificial selection occurs, with some exceptions, under conditions of high resource availability, the transfer of modern crops into low input agricultural systems is often impeded or challenging (Warschefsky et al., 2014). Many growth-supporting soil physical and chemical characteristics can change significantly when shifting from conventional to organic production, where mineral fertilizer and pesticide inputs are minimized (Mäder et al., 2002; Chen et al., 2018). As an integrated approach, organic farming seeks to manage soil fertility using ecological approaches by enhancing crop production through a greater reliance on biotic interactions and the mineralization of organic inputs, rather than relying on off-farm chemical inputs (Drinkwater and Snapp, 2007; Heckman et al., 2009). In turn, soil environments in organic systems are characterized by slow release of nutrients derived from organic sources which are supported by, or a direct consequence of, (1) longer and more complex crop rotations, (2) coupled carbon and nutrient cycles, (3) holistic farm management, and (4) ecological approaches to pest management.

In organic systems amendments such as composts, manures, and cover crops are a primary source of crop nutrients, with rates of nutrient availability and transfer supported by soil biological mineralization and microbial community interactions. Indeed, in many cases even inorganically fertilized crops obtain 50% of their nitrogen (N) from biologically mineralized organic N pools (Gardner and Drinkwater, 2009; Yan et al., 2020). But while inorganic fertilizers tend to reduce soil organic carbon (C) and microbial biomass, organic amendments generally enhance soil physiochemical properties including soil organic matter (SOM) and microbial biomass (Drinkwater and Snapp, 2007). In turn, enhanced SOM from organic amendments contributes to the retention of plant-available nutrients and water, maintenance of soil structure, and sources of soil phosphorus (P) and total N contents, but these contributions tend to be highest in soils with initially low fertility (Chen et al., 2018). Importantly, the positive effects of organic amendments on microbial biomass -the agent of nutrient mineralization (Cayuela et al., 2009)–do not consistently and predictably increase crop nutrient uptake, in part because of the complex three-way interactions between crops, soil nutrient pools, and soil microbial communities. For example, crops can vary in their ability to compete with soil biota for nutrients, or modify their root environment and associated soil biota to be favorable for organic mineralization.

Crop Trait Variation and Organic Management

Due to relatively limited efforts in breeding crops explicitly for organic systems, most organic farmers in North America currently use modern cultivars that were bred for use in conventional high-input production systems (Murphy et al., 2007). As a result, organic breeding represents an unexplored frontier in crop breeding and ecophysiology. Indeed, understanding and managing the plant-soil-microbial interactions in organic systems with greater precision could contribute to the development of crop cultivars that respond preferentially to organic soil environments. However, due to unique soil systems present in organic vs. conventional systems, plant traits that are of interest to organic crop breeding may differ widely from those favored by conventional crop breeding. Undoubtedly, plant traits selected over the course of long domestication histories can have significant legacies for nutrient acquisition strategies (**Figure 1**).

Selection for crops that express certain reproductive, leaf, and root traits has formed detectable, albeit diverse, domestication syndromes: suites of plant traits which differ between crops and their wild progenitors. However, scientific and informal on-farm research has primarily focused on understanding and managing linkages between only certain domestication traits and yield, particularly under conventional agricultural management systems (Meyer et al., 2012). There is strong evidence suggesting that functional traits—i.e., the morphological (e.g., leaf area), physiological (e.g., photosynthesis), and chemical (e.g., N concentrations) traits of plants—can be used to hypothesize and detect trade-offs, constraints, and synergies among crop yield, other aspects of crop biology, and agroecosystem function (Martin and Isaac, 2015). Functional trait-based studies have also been instrumental in advancing our understanding of observable ecological patterns, e.g., relationships between on-farm diversity and agroecosystem processes, while providing a framework for predicting future agroecosystem responses to environmental change (Lavorel and Garnier, 2002; Damour et al., 2018). Yet while the literature exploring trait-based

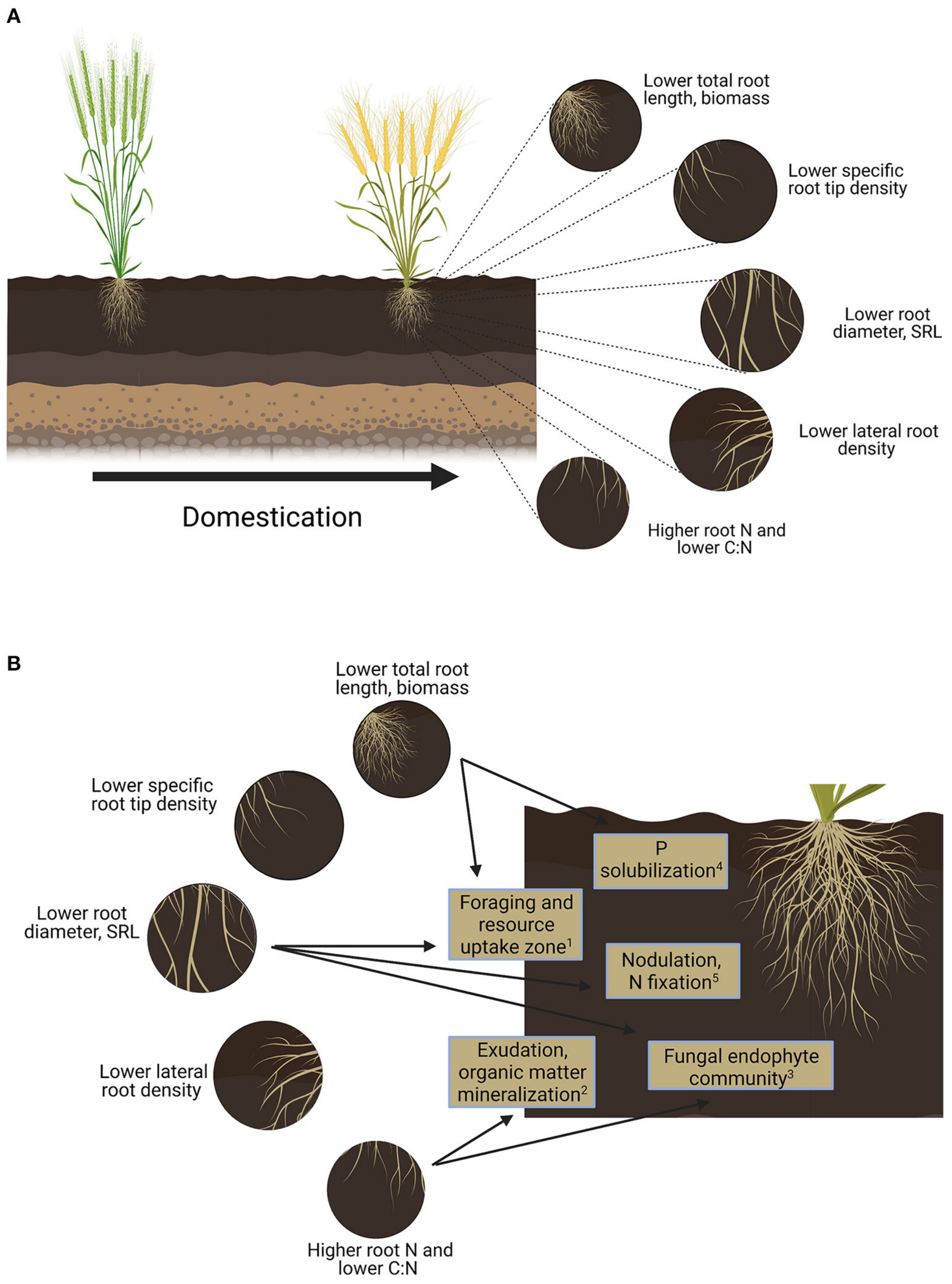

FIGURE 1 | Hypothesized root functional trait syndromes via selection through domestication **(A)** and hypothesized effects of selected root traits on rhizosphere functions **(B)**. This figure was created with BioRender [1Cahill et al., 2010; 2Herz et al., 2018; 3Fulthorpe et al., 2020; 4Bargaz et al., 2017; 5Martin et al., 2019].

agroecology is growing (Martin and Isaac, 2018), to date no studies have explicitly summarized existing literature and data, in order to propose hypotheses on (1) how and why traits are expected to shift within and among crops in organic vs. conventional system; and (2) how changes in traits and trait syndromes may influence crop nutrient acquisition strategies in organic systems.

Crop Trait Variation and Domestication Syndromes

In agricultural systems, studies have evaluated how interspecific (Buchanan et al., 2020; Gagliardi et al., 2020) and intraspecific (Isaac and Martin, 2019; Coleman et al., 2020; Sauvadet et al., 2021) trait variation are mechanistically linked with agroecosystem functioning. Others have also applied a functional traits lens to understand the impacts and outcomes of crop domestication. For example, through domestication crops tend to express traits associated with higher rates of resource capture—namely greater aboveground biomass, higher whole-plant photosynthetic rates, greater leaf area, and higher specific leaf area (SLA)—as compared to their wild progenitors (Milla et al., 2014). Milla and Matesanz (2017) showed that crop domestication was associated with a general increase in certain crop physiological and chemical traits, including leaf-level photosynthesis and leaf N concentrations, but there were mixed results among crop species. The lack of evidence for systemic shifts in leaf photosynthesis and N concentrations through domestication may owe to multiple factors, such as total N uptake being diluted by a greater plant biomass (Wacker et al., 2002), or crop progenitors already exhibiting leaf traits on the acquisitive end of trait strategies (Milla et al., 2015).

In comparison, shifts in root functional traits throughout domestication have largely been overlooked. It appears that relationships between root functional traits, including specific root length (SRL), specific root area (SRA), root N, and root diameter (D), and plant resource acquisition strategies are arguably more complex than leaf trait trade-offs (Isaac and Borden, 2019). For instance, root trait responses to resource gradients are often confounded by collaboration gradients with soil microbial populations and diversity (Bergmann et al., 2020). Broadly though, it is often hypothesized that compared to wild relatives, crops allocate less biomass to below- vs. aboveground biomass as a result of (1) abundant soil resources, and (2) reduced herbivory pressures in agricultural systems. Importantly, some studies show that semi-dwarf cultivars, which have been a large part of cereal domestication, have shown little effects on root growth but some effects on root activity (Gentile et al., 2005). However, one may hypothesize that consistent shifts in root trait values have occurred in crops with domestication (**Figure 1**). Specifically, owing to domestication in high resource environments, crops may have greater investment to individual roots. This general pattern is expressed by the following morphological trait syndromes in crops: (1) lower root D, paired with (2) low SRL, lateral root density, and specific root tip density. These morphological traits can also be associated with crops expressing certain root chemical traits including (1) higher root N concentrations, and (2) lower root C:N ratios. Each of these shifts in root trait expression can be linked to multiple spatial, biochemical, and microbial factors within soil environments, with well-established links to nutrient acquisition success.

Domestication Syndromes, Root Functional Traits, and Organic Agriculture

While literature supports hypotheses surrounding (1) how root traits have changed through the course of crop domestication, and (2) how those root trait syndromes might be expected to influence nutrient acquisition with ecological management, there are few studies that have integrated these two themes. Therefore, here, we seek to chart new territory in the areas of crop breeding and organic management, by synthesizing knowledge on the following questions: (1) has domestication systematically influenced root functional traits in crops vs. wild progenitors?; and if so (2) do root traits have a hypothesized influence on nutrient acquisition in low input systems? Assessing these questions then informs our final question: (3) have transformations toward low input organic systems reframed questions of domestication syndromes in crops?

METHODS

To assess our first question, we extracted and analyzed bivariate correlations among three root traits including SRL, root N, and root D, by consolidating data on four crops and their wild progenitors. Data were extracted from the Global root traits (GRooT) database (Guerrero-Ramirez et al., 2021) and included: (1) rice (*Oryza sativa*) and its wild relative *O. rufipogon*; (2) durum wheat (*Triticum durum*) and its wild relative *T. dicoccoides*; (3) maize (*Zea mays*) and wild relative *Z. mays mexicana*; and (4) grass species *Panicum virgatum* (crop) and *P. capillare* (wild). We compared patterns of root trait trade-offs with patterns observed in all species in the GRooT database in bivariate figures depicting SRL as a function of root D ($n = 1,460$) and root N ($n = 1,247$). This root trait data was pooled into figures depicting root trait trade-offs.

We also consolidated data from peer-reviewed papers that quantified root traits in both wild progenitors and domesticated crops. In these papers, plants were grown in the same conditions and traits measured in the same way, thus providing a case by case comparison of effects of domestication on root traits. This systematic review uses a PICO formula: population (crop functional traits), intervention (domestication), comparison (wild plants to artificially selected plants) and outcome (nutrient acquisition). We searched the Web of Science database for terms included in our PICO formula [root trait* AND domestication], which resulted in 200 papers published over the past 20 years. Of these 200 papers, 11 met the following inclusion criteria: papers had to present paired data on wild relatives and domesticated crops grown in similar conditions, and include at least one measure of SLA, root N, root D, or total root length (TRL). We then conducted citation mining on all 11 papers, and with this approach included another three papers. This resulted in a total of 14 papers used in our analysis here (**Table 1**). Data was compiled from tables and figures in manuscripts and supplementary files, and consolidated and analyzed to depict the percent change (positive or negative) in root trait values (SLA, TRL, root D, root N) between wild relatives and paired domesticated crop. Finally, we used outcomes from our systematic review to inform hypotheses on how domestication syndromes of root traits may impact nutrient acquisition in low input and organic systems, which rely on ecological processes for crop nutrient supply.

RESULTS AND DISCUSSION

Root Trait Patterns Globally

Crop root traits co-vary in patterns consistent with established trait trade-offs in wild plants globally (**Figure 2**). In bivariate space, root D and SRL are negatively correlated, such that

TABLE 1 | Sources identified through a systematic literature review, with associated wild relative, crop and suite of root traits in each source.

Source	Wild relative	Crop	Root traits
Nakhforoosh et al., 2021	*Triticum dicoccoides*	*Triticum durum* (durum wheat)	SRL; TRL
Marques et al., 2020	*Cicer reticumlatum*	*Cicer arietinum* (chickpea)	SRL
Schmidt et al., 2020	Pre1942 *Zea mays mays* hybrids	Post 1942 *Zea mays mays* hybrids (maize)	TRL; root N
Barel et al., 2019	*Arrhenatherum elatius*	*Avena sativa* (oat)	Root N
	Festuca rubra	*Lolium perenne* (ryegrass)	
	Trifolium pratense	*Trifolium repens* (clover)	
	Vicia cracca	*Vicia sativa* (vetch)	
	Raphanus raphanistrum	*Raphanus sativus* (fodder raddish)	
	Cichorium intybus	*Cichorium endive* (endive)	
Berny Mier y Teran et al., 2019	Wild *Phaseolus vulgaris*	*Phaseolus vulgaris*	SRL
Martín-Robles et al., 2019	*Cicer reticulatum*	*Cicer arietinum* (chickpea)	SRL, root D
	Zea mexicana	*Zea mays mays* (maize)	
	Triticum dicoccoides	*Triticum durum* (durum wheat)	
Pastor-Pastor et al., 2019	*Physaria pinetorum* *Physaria mendocina*	*Physaria* (high seed-yield accession)	SRL; root N
Junaidi et al., 2018	*Aegilops tauschii*	*Triticum aestivum* (wheat)	SRL, root D, TRL
Roucou et al., 2018	*Triticum dicoccoides*	*Triticum durum* (durum wheat)	SRL, root D
Pérez-Jaramillo et al., 2017	Wild *Phaseolus vulgaris*	*Phaseolus vulgaris* (bean)	SRL
Chinchilla-Ramírez et al., 2017	*Zea mays parviglumis*	*Zea mays mays* (maize)	TRL
Gioia et al., 2015	*Triticum dicoccoides*	*Triticum durum* (durum wheat)	TRL
Szoboszlay et al., 2015	*Zea mays parviglumis*	*Zea mays subsp. mays* (maize)	TRL, root D
Gaudin et al., 2011	*Zea mays parviglumis*	*Zea mays mays* (maize)	SRL, TRL

TRL, Total Root Length; SRL, Specific Root Length; root N (nitrogen); root D (diameter).

species expressing large root D and low SRL fall on the resource conservative end of the relationship, and species expressing high SRL and constrained root D fall on the resource acquisitive end of the relationship. Broadly, wild relatives express more resource acquisitive root traits compared to their domesticated counterparts, with systematic shifts toward resource conservation in crops, especially for rice and maize.

Root trait variation between wild relatives and domesticated crops is a function of conscious and unconscious artificial selection and in response to soil environments (Zohary, 2004). The wild progenitors of many crops already existed in the acquisitive end of the root economic spectrum (Milla et al., 2015), but here we show a shift toward resource conservation in root trait expression with domestication. This finding is (1) counter to evidence from studies on leaf traits, which are shown to express leaf-level trait values that reflect highly resource acquisitive strategies with domestication (Cunniff et al., 2014; Milla et al., 2015); but (2) supports the meta-analysis of Martín-Robles et al. (2019) which illustrated diverse directions of change in root traits with domestication, with no systematic pattern among plant functional groups. Complicating factors include the nature and relative recency of shifts in soil environments, primarily increased use of N and P fertilizers in the last ∼100 years, compared to the effects of millennia of selection on other traits such as seed size (Meyer et al., 2012; Abbo et al., 2014). Disentangling and isolating the effects of domestication *per se* on root traits is further complicated due to the impacts of farm management techniques such as tilling (Fiorini et al., 2018), and soil physical properties (Borden et al., 2020), on root traits.

Changes in Crop Root Functional Traits With Domestication–Data Comparison

We compared trait values of domesticated crops and their wild relatives, covering a range of crop-wild relative complexes including wheat (*Aegilops tauschii*), durum wheat (*Triticum durum* ssp. *dicoccoides*), maize (*Z. mays mexicana*), Chickpea (*Cicer reticulatum*). **Figure 3** illustrates the percent change in root trait values through domestication, ordered by phylogenetic relatedness. Results from published literature are mixed. In some instances, SRL, TRL, root D, and root N values are higher in wild relatives vs. crops, while the opposite pattern is true for other crop-wild relative combinations. However, root D is generally larger in wild relatives vs. crops, expressing a negative percent change in trait values with domestication. Interestingly, SRL tends to have positive percent change in trait values with domestication, indicating a shift toward higher SRL in domesticated crops as compared to wild relatives (**Figure 3**). However, this trend is opposite for leguminous species *Phaseolus*: the percent change in trait values through domestication for beans is consistently negative.

These shifts in root trait values reported between paired domesticated crop traits with wild relatives, are not consistent with trends reported from global datasets as shown in **Figure 2**. While these trends of crops and wild relatives fall into established trait trade-off patterns, they do not reflect the nuances of pairing crops and wild relatives in the same growing conditions with the same measurements. In doing so here, we show a clearer trend of domesticated crops expressing acquisitive traits (higher SRL and lower root D) than those compiled from unpaired global datasets; a finding that is more consistent with leaf trait changes that occur through domestication. Our paired data highlights another critical area of root trait shifts as a result of domestication: the strength of relationships between root traits and arbuscular mycorrhiza. Older crop varietals may be more able to form these symbiotic relationships regardless of nutrient availability, while modern varietals only benefit

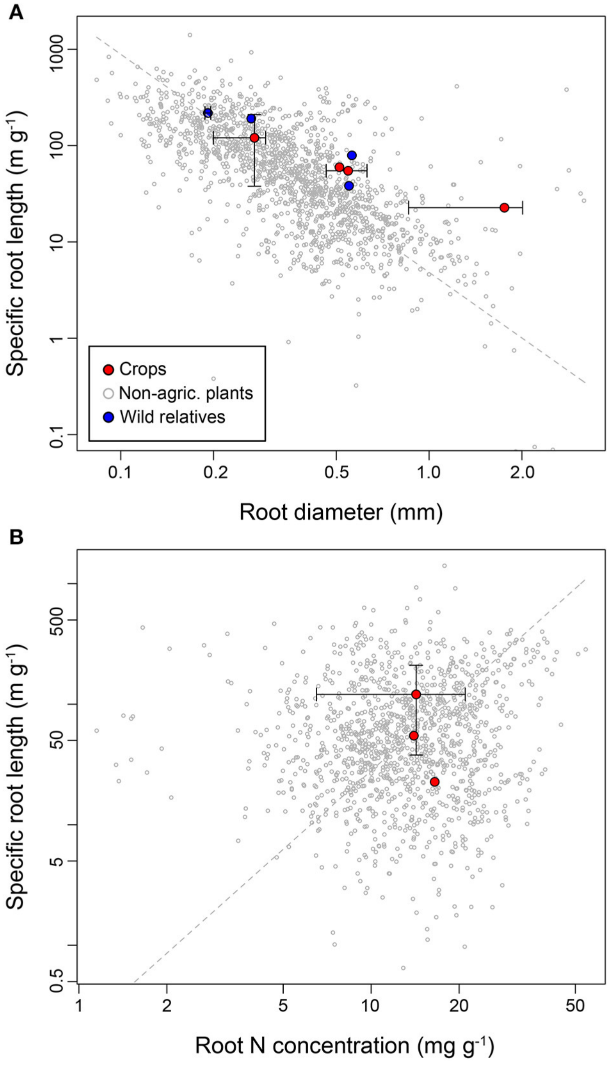

FIGURE 2 | Bivariate relationships among root traits [root diameter and specific root length **(A)** and root N and specific root length **(B)**] of crops. In order to visualize the extent of root trait trade-offs, crops and their wild relatives are included, as well as trait relationships observed across the whole GRooT dataset (Guerrero-Ramirez et al., 2021).

from the symbiosis when under nutrient stress (Martín-Robles et al., 2018). Plant-microbial symbiosis that destabilize systematic trait trades-offs (Bergmann et al., 2020), are not consistently accounted for in trait databases when pairing data from unrelated studies, though these relationships are key factors underpinning root trait expression and covariation.

Hypothesized Outcomes for Nutrient Acquisition

Variation in root traits may either facilitate or inhibit organic nutrient mineralization and nutrient acquisition. Plants exhibit diverse root acquisition strategies to enable nutrient uptake, including mechanisms that regulate nutrient bioavailability (Hinsinger, 2001), supply rates (Isaac and Kimaro, 2011), and foraging and absorption (Borden et al., 2020). Some of these mechanisms are complementary in order to enable acquisition of nutrients with different mobility and availability through time and space (Lambers et al., 2008; Lynch, 2019). Shifts in root traits with domestication will have explicit effects on the success of nutrient acquisition in low input organic systems (**Figure 1**).

Specifically, higher SRL and TRL are linked with foraging and higher resource uptake zones (Cahill et al., 2010), which could complicate soil nutrient acquisition in organic systems. In contrast, overall higher root biomass is associated with higher phosphate-solubilizing enzyme activity (Bargaz et al., 2017), which benefits plant P acquisition in low-input organic systems. How root exudation varies among root traits is not yet resolved, though several studies suggest an increase in exudation and SOM mineralization, with smaller root D, higher root N concentrations, and higher SRL (Guyonnet et al., 2018; Poirier et al., 2018; Han et al., 2020; Henneron et al., 2020). Although root traits associated with rapid nutrient acquisition are more likely to dominate when inorganic nutrient supply is high, root exudation is expected to increase under low nutrient supply as more biomass is allocated to roots (Herz et al., 2018). Chemically, root exudate composition has been shown to co-vary with root traits, with lower C:N exudates associated with high resource acquisitive traits (Herz et al., 2018). Root exudation is a significant mechanism regulating nutrient mobilization and mineralization by providing soluble C and nutrients that can stimulate soil microbial activity (Meier et al., 2017). Root exudates can also stimulate the release of N from mineral-associated organic matter into soil solution, further accelerating microbial activity that drives nutrient mineralization (Jilling et al., 2018). This is of particular interest for organic and low-input agricultural systems, because lower C:N exudates may cause a stronger stimulatory effect on nutrient mineralization when available N is more limited in organic systems, compared to conventional high-input cropping systems.

Systematic shifts in crop root traits can also indirectly affect nutrient availability and acquisition by altering soil microbial community composition (Cantarel et al., 2015). For example, SRL and root D have been shown to predict total arbuscular mycorrhizal fungi (AMF) colonization, which can greatly enhance nutrient supply to the host plant (Wen et al., 2019; Sweeney et al., 2021). In diversified agricultural systems, higher root D and root C:N, as well as low root N concentrations, were strong predictors for fungal endophyte community composition (Fulthorpe et al., 2020), while higher SRL and lower root D of legumes were associated with higher counts of root nodules formed in symbiosis with diazotrophic microorganisms (Martin et al., 2019). Undoubtedly, domestication effects on root trait values, trade-offs, and their relationships with microbial communities, are essential in understanding crop success when transferred to organic production. Under ecological nutrient management, coupling microbial activity and mineralization with plant nutrient uptake tends to decrease potential for nutrient losses (compared to inorganic fertilizers), thus, contributing another important factor in achieving environmental sustainability of agriculture.

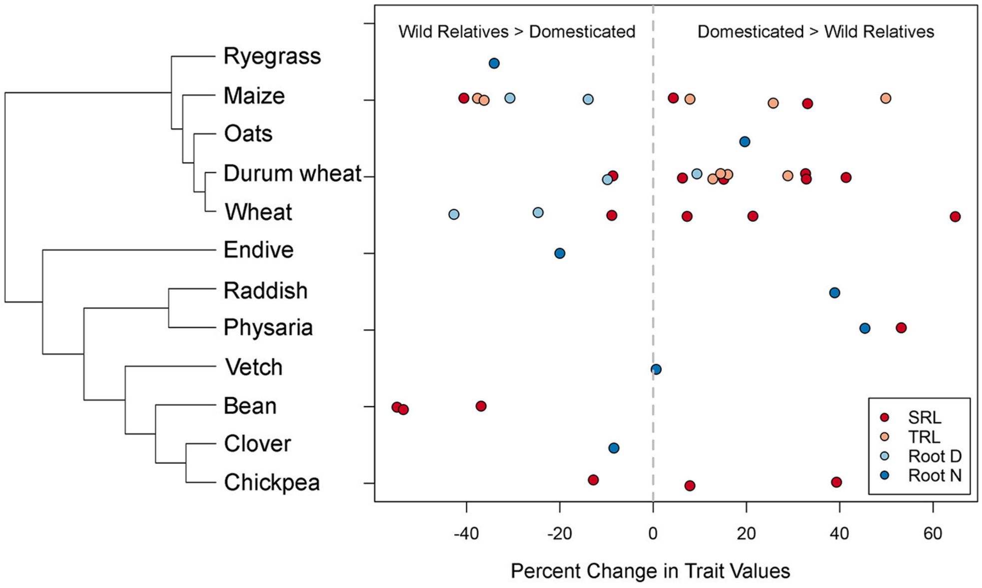

FIGURE 3 | Percent change in trait values for 12 crops, organized according to their phylogenic relationships, and their paired wild relatives. Specific root length (SRL), total root length (TRL), root diameter (root D), and root nitrogen (root N) are depicted.

BOX 1 | Three decades of organic agriculture research at Glenlea, Manitoba, Canada.

Factors affecting plant nutrient acquisition in organic production have been studied in the Canadian context at the Glenlea study for three decades. Within the first 15 years of organic production, researchers observed a shift in the soil P pools, with less plant available P (Welsh et al., 2009) and more organic P (Braman et al., 2016). This could either suggest relatively higher plant P uptake thus reducing the soil available P pool, or alternatively slower cycling of organic P into the plant availability P pool. Root traits (through their exudation, associations with mycorrhizae, and architecture) can significantly increase rates of P cycling along with P acquisition. However, to optimize this in organic and low-input systems, breeding should consider targeting root traits that will support these interactions. At Glenlea, the soil biological community appears to be mineralizing organic P faster, suggesting that the lower plant P availability in the organic systems is likely related to more rapid P mineralization coinciding with rapid plant P uptake. Indeed, microbial P was more responsive to soil wetting after drought in organic than in conventional production (Braman et al., 2016). The increase in mycorrhizal colonization in organic crops (Entz et al., 2004), and the decline in abundance of non-mycorrhizal weeds (Carkner et al., 2020) were both attributed to less available P. Greater mycorrhizal colonization may have been one reason for greater zinc uptake in organic compared with conventional wheat at Glenlea (Turmel et al., 2009). Enzymes play an important role in plant nutrient acquisition. Fraser et al. (2015a,b) observed greater alkaline phosphatase activity in the low available P conditions at Glenlea, and linked greater alkaline phosphatase activity with bacterial *phoD* gene abundance in soil. Organic systems also had higher levels of dissolved carbon (Xu et al., 2012) and carbon mineralizing enzyme activities (unpublished). Organic systems at Glenlea maintained a more neutral pH (Welsh et al., 2009) which was linked to changes in the soil bacterial community (Li et al., 2012). These chemical and biological factors can strongly affect plants' ability to acquire nutrients through the management of ecological processes.

Acquisition strategies emerging through domestication may be confounded by nutrient allocation patterns within crops (Løes et al., 2020). For instance, there is a well-known dilution effect of minerals in modern wheat grains conferred from higher yields (Zhao et al., 2009), and studies have recently shown that nutritional quality is lower in crops compared to wild relatives (Fernandez et al., 2021). Although acquisition strategies may change with domestication and translate to highly variable nutrient uptake across conventional vs. organic systems, the resulting effects on yield are not as systematic. Additionally, wild plants are adapted to grow under more stressful environmental conditions, and thus are likely to allocate greater resources to constitutive or inducible defenses: Fernandez et al. (2021) showed that higher herbivory and lower investment in defense was a common feature of crop domestication. Given controls from nutrient allocation patterns within crops from wild progenitor to modern cultivars, and stronger resource allocation toward plant defense in wild progenitors, one would hypothesize uneven relationships between root traits and yield, and between defense and yield, in crops vs. wild plants.

Implications of Root Trait Variation for Breeding Programs for Ecological and Organic Nutrient Management

Due to the inherent and multi-faceted differences in growing environment between organic and conventional production systems (see **Box 1** for a long-term research case study on soil biochemistry in organic vs. conventional systems), increased efforts in organic breeding have the potential to reduce the yield gap by developing crop cultivars that respond well to organic environments. For instance, the spatial and temporal heterogeneity in organic agricultural soils requires crops with high root plasticity, which in turn confers an advantage for successful nutrient acquisition in low-input systems. Conventional seeds often perform poorly in organic agricultural systems (Boyle, 2016), in terms of leaf area and root mass development, root branching, nutrient use efficiency, and, in the case of legumes, nodulation. Such factors makes crop breeding for organic production difficult but essential.

Cultivar selection is a critical aspect for organic farmers to consider in relation to soil fertility, as well as pest and weed management (Bond and Grundy, 2001; Watson et al., 2002; Zehnder et al., 2007; Lammerts van Bueren and Myers, 2012; Entz et al., 2018). Building on approaches suggested by Crespo-Herrera and Ortiz (2015) for developing new cultivars for organic systems, such as (i) multi-location testing to exploit Genotype × Environment interactions, (ii) shuttle breeding between organic and conventional production systems to develop cultivars adapted to both conditions, and (iii) comprehensive screening of plant materials deposited in gene-banks to identify promising genetic resources for organic plant breeding, we highlight the need for increased understanding of the variation and genetic architecture of root traits important for crop success under organic conditions. In particular, there remains a critical need for breeding programs that explicitly focus on organic agriculture by better understanding relationships between domestication syndromes, root trait expression, and nutrient acquisition strategies in low input systems.

Drawing on global datasets and published data, we show detectable shifts in root trait strategies with domestication. Relationships between domestication syndromes in root traits, and the subsequent impact on acquisition strategies in low input systems, underscores the need for a shift in breeding paradigms for organic agriculture. Such efforts are under way in many different field and horticultural crops, for instance in Canada for wheat (Wiebe et al., 2016; Entz et al., 2018), oats (Mitchell Fetch et al., 2021) and soybean (Boyle, 2016). As the call for transformations in agricultural management reaches a watershed moment, in order to achieve SDG targets of Zero Hunger via resilient agriculture practices, these efforts will not only enhance multiple ecosystem services in organic agriculture, but also amplify the success of ecological nutrient management.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

MI conceived and coordinated the study. JS generated the illustration. AM generated the figures. All authors contributed to the formulation of ideas, manuscript writing, and final approval for publication.

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Toward Zero Hunger Through Coupled Ecological Sanitation-Agriculture Systems

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Ecological sanitation (EcoSan) systems capture and sanitize human excreta and generate organic nutrient resources that can support more sustainable nutrient management in agricultural ecosystems. An emerging EcoSan system that is implemented in Haiti and several other contexts globally couples container-based household toilets with aerobic, thermophilic composting. This closed loop sanitation system generates organic nutrient resources that can be used as part of an ecological approach to soil nutrient management and thus has the potential to contribute to Sustainable Development Goals 2 (zero hunger), 6 (clean water and sanitation for all), and 13 (climate change solutions). However, the role of organic nutrient resources derived from human excreta in food production is poorly studied. We conducted a greenhouse experiment comparing the impact of feces-derived compost on crop production, soil nutrient cycling, and nutrient losses with two amendments produced from wastewater treatment (pelletized biosolids and biofertilizer), urea, and an unfertilized control. Excreta-derived amendments increased crop yields 2.5 times more than urea, but had differing carry-over effects. After a one-time application of compost, crop production remained elevated throughout all six crop cycles. In contrast, the carry-over of crop response lasted two and four crop cycles for biosolids and biofertilizer, respectively, and was absent for urea. Soil carbon concentration in the compost amended soils increased linearly through time from 2.0 to 2.5%, an effect not seen with other treatments. Soil nitrous oxide emissions factors ranged from 0.3% (compost) to 4.6% (biosolids), while nitrogen leaching losses were lowest for biosolids and highest for urea. These results indicate that excreta-derived compost provides plant available nutrients, while improving soil health through the addition of soil organic carbon. It also improved biogeochemical functions, indicating the potential of excreta-derived compost to close nutrient loops if implemented at larger scales. If captured and safely treated through EcoSan, human feces produced in Haiti can meet up to 13, 22, and 11% of major crop needs of nitrogen, phosphorus, and potassium, respectively.

Keywords: ecological sanitation, greeenhouse-gas (GHG) emission, soil carbon, excreta, compost, sustainable develop goals

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INTRODUCTION

Nutrient recovery from organic waste streams and recycling in agriculture is a critical component to achieving Sustainable Development Goal (SDG) 2, which aims to eliminate hunger (Springmann et al., 2018; Gerten et al., 2020). Current linear modes of fertilizer provision rely on external inputs of nutrient, energy, and water for agricultural production, and non-harvestable resources are predominately wasted and/or lost to the environment. This linear model has local to global consequences for human and ecosystem health. The production and intensive use of fertilizers have perturbed biogeochemical cycles to the extent that the planetary boundary for global nitrogen (N) and phosphorus (P) cycles has already been exceeded (Steffen et al., 2015). Nitrogen fertilizers are produced from the energy-intensive Haber-Bosch process, which converts unreactive atmospheric N in the form of dintrogen (N_2) to a reactive form of N, ammonia (NH_3). This synthetic fixation of N has more than doubled the amount of N that cascades through the environment in different forms of reactive N (Fowler et al., 2013). Only 4 to 14% of N applied to crops is consumed by humans, with the rest lost to watersheds and the atmosphere (Pikaar et al., 2017). Excess reactive N in the form of nitrate contributes to the eutrophication of water systems and contamination of groundwater. Gaseous nitrous oxide (N_2O) is a global warming pollutant and contributes to stratospheric ozone depletion and nitrogen oxides (NO_x) contribute to smog and acid rain (Zhu and Chen, 2002; Erisman et al., 2013). Similarly, rock phosphate, the predominant source of phosphorus (P) fertilizers, is a non-renewable resource mined from spatially heterogenous mineral reserves (Cordell and White, 2014). Phosphate rock is a finite resource that will eventually be depleted, although recent estimates indicate no imminent scarcity of these reserves based on future rates of consumption (USGS, 2021). Excess phosphorus that is not taken up by plants can bind to sediments, produce P-rich runoff, and eutrophy water bodies (Sharpley and Menzel, 1987).

The provision of nutrients is a critical component of sustaining agricultural production (Tully and Ryals, 2017). While the extensive production and use of mineral fertilizers was an intentional strategy of the Green Revolution to alleviate hunger, it came at a heavy cost to the quality of air, water, and soil resources (Pingali, 2012). Additionally, hunger and malnutrition have persisted despite the continued increase in fertilizer use. A shift away from inorganic fertilization with synthetic and mined resources toward organic fertilization with natural byproducts and end products could alleviate some pressure on N and P planetary boundaries through reduced nutrient loading to the environment (Drinkwater and Snapp, 2007; Eden et al., 2017; Springmann et al., 2018). Recycling organic waste streams to agricultural soils can provide plant available nutrients to support crop or forage production as well as organic matter to improve soil health and ecosystem services. Therefore, ecological approaches to nutrient management reduce waste and foster more resilient agroecosystems (Schipanski et al., 2016), one of the targets of SDG 2.

The capture and transformation of human excreta represents an enormous and largely untapped strategy for circular models of nutrient management (Harder et al., 2019, 2020; Theregowda et al., 2019). Global production of human feces is projected to pass 1 Pg of wet matter per year (Berendes et al., 2018). Though excreta recovery has been practiced throughout cultures and history (Angelakis et al., 2018), this practice has been largely discontinued due to the advent of centralized wastewater treatment systems and inexpensive inorganic fertilizers (Bracken et al., 2007). The current low cost of synthetic N fertilizer can be attributed to fossil-fuel derived hydrogen, which is used in the Haber-Bosch reaction, and is likely to increase in the coming decades as society shifts away from fossil fuels. Alternative sources of N, including N recovered from human excreta, have the potential to be economically feasible, especially if externalities are accounted for. Feces and urine are nutrient-rich waste streams, with feces containing the majority of excreted carbon (C) and approximately half of P and potassium (K), and urine the majority of excreted N and the remaining P and K (Harder et al., 2019). Distinct treatment of feces and urine requires source separation, a method that is not currently practiced on a large scale in Western societies (Larsen et al., 2013).

One area of resource recovery research is on biosolids, the organic residue from wastewater treatment that results from mixed streams. The agronomic benefits and tradeoffs of nutrient recycling from biosolids have been extensively studied (e.g., Wang et al., 2008; Lu et al., 2012). Recent reviews of biosolids land application highlight the relationship between biosolids and ecosystem services, especially those linked to soil health, and the socioeconomic value of circular sanitation economies (Trimmer et al., 2019; Toffey and Brown, 2020). Diverting biosolids from landfills also contributes to climate change mitigation by reducing landfill methane emissions (Brown et al., 2008) and, when land applied, increasing stocks of carbon (C) in soil (Torri et al., 2014; Villa and Ryals, 2021). Land application of treated biosolids is a common practice, but there remains considerable potential to further recover and safely recycle biosolids nutrients. For example, the United States already incorporates 55% of all treated sewage sludge back onto agricultural lands but continues to landfill 30% and incinerate 15% of all sludge produced (Peccia and Westerhoff, 2015). Regulations aimed at minimizing public health risks of potential pathogens, persistent pollutants, and contaminants limit the application amount, timing, and frequency of biosolids land application, yet regulatory limits vary among regions and countries (Gianico et al., 2021). Historically, regulatory limits were based on concentrations of heavy metals and pathogen loading. More recently, emerging contaminants, like pharmaceuticals, have also driven regulatory limits or concerns over biosolids land application, and knowledge gaps remain about the impact of contaminants like microplastics (Clarke and Cummins, 2015).

Compared to biosolids, less research is available on effective nutrient recycling from non-sewered sanitation systems. This is an important gap in knowledge that could inform ecological approaches to nutrient management in regions and societies experiencing underdevelopment following colonization. Approximately 4.2 billion people globally lack access to safely managed sanitation. Of this population, ∼2 billion people globally lack access to basic sanitation and 673 million people practice open defecation [World Health Organization, and (WHO) and the United Nations Children's Fund (UNICEF), 2020]. Global flows of wasted human excreta N, P, and C are highly uncertain, but estimates clearly indicate the significance of non-sewered systems to nutrient imbalances, particularly in low and middle income countries. Between 85–93 and 77–90% of the N and P, respectively, excreted by humans in low and middle income countries is released into the environment without treatment (Fuhrmeister et al., 2015), wasting valuable nutrient resources and causing severe consequences for human and ecosystem health. Conventional sewage that uses fresh water to move and treat human waste is unlikely to meet many of these sanitation needs for several social, economic, and ecological reasons (Öberg et al., 2020). Likewise, current forms of non-sewered sanitation systems that do not ensure safe and effective treatment and land application do not meet societal and environmental health goals, and are not considered ecological nutrient management (Guo et al., 2021). Managing sanitation in a changing climate is a challenge, particularly when systems rely on large quantities of fresh water and centralized, extensive infrastructure that requires significant capital and trained management (Kohlitz et al., 2017). Global efforts to enhance access to adequate sanitation under SDG 6 are driving demand for innovative non-sewered sanitation services, particularly in regions that are rapidly urbanizing and where water resources are scarce (Russel et al., 2019; McConville et al., 2020).

Ecological sanitation (EcoSan) systems have the potential to transform nutrient management by explicitly coupling sanitation and agriculture (Langergraber and Muellegger, 2005; Haq and Cambridge, 2012). EcoSan refers to a suite of practices that aim for closed-loop management of human excreta. EcoSan designs are often non-sewered and feature separate collection and treatment of urine and feces. These systems have been implemented throughout the world, but with tremendous potential for growth (GIZ, 2012; Hu et al., 2016). EcoSan may reduce public health risks while creating a locally accessible source of nutrients, thus increasing food security and agroecosystem sustainability, and bolstering local circular economies (Langergraber and Muellegger, 2005). There is particularly high potential for the implementation of EcoSan in emerging urban environments with dense populations located near cropland, which may help offset mineral fertilizer imports (Trimmer and Guest, 2018). Recommendations for optimal designs of EcoSan systems based on local socio-economic and cultural contexts and safety guidelines have been developed to encourage the adoption of EcoSan services (Reed and Shaw, 2003; WHO, 2006; Simha and Ganesapillai, 2017). However, several interrelated economic, institutional, and political barriers need to be overcome in order to realize large-scale adoption of EcoSan (Sinharoy et al., 2019). In the context of nutrient management, the lack of data on the use of novel organic amendments from EcoSan limits understanding of effects on crop production, nutrient cycling, and water quality effects, which impairs decision makers and inhibits widespread adoption (Smith et al., 2016).

An emerging EcoSan system that has been modeled in Haiti and other low resource settings couples container-based toilets with aerobic, thermophilic composting. This model of EcoSan has been demonstrated at medium-scales (∼9,000 toilet users per day in 2020) by the non-profit organization, Sustainable Organic Integrated Livelihoods (SOIL), in Haiti since 2006. SOIL's container-based sanitation (CBS) technology separates urine and feces on-site. Feces are combined with a sugarcane residue and transported to a centralized compost facility for sanitization and processing. Aerobic, thermophilic composting of human feces is effective at reducing pathogenic loads to safe levels, which can help achieve public health goals (Berendes et al., 2015; Piceno et al., 2017). Coupled sanitation-agriculture systems that return both nutrients and organic matter to soil can be particularly beneficial in regions that experience severe soil degradation, food insecurity, and climate vulnerability (Bargout and Raizada, 2013). The most severe impacts of these factors are found in Haiti, where 61.9% of the population cannot afford a nutrient adequate diet, 48.2% of the population is undernourished, and which is not currently on track to meet SDG 2 (FAO, IFAD, UNICEF, WFP and WHO, 2020). Progress on SDG6 is also falling short, as only 37.1% of people have access to basic sanitation services, which means having access to a sanitation facility that is not shared with other households but does not include the safe treatment or disposal of waste (United Nations, 2021). In the Cap Haitïen, the second most populous city in Haiti, only 1% of human excreta is safely managed, primarily by SOIL's EcoSan service (Biscan, 2018). The cause of these vulnerabilities are deeply rooted in the country's institutional and environmental colonial legacy (Dubois, 2013). After the Haitian Revolution succeeded in ending slavery and winning independence from France, the country was forced to pay reparations to their enslavers over the next 100 years, draining financial capital and investment. Further, the birth of Haiti as an independent nation had little support from other nations. The US did not recognize it until 1862, and occupied the country from 1915 through 1934. High rates of deforestation, soil infertility, and natural resource depletion are strongly tied to Haiti's political ecology (Baro, 2002). Thus, the restoration of Haiti's soils through circular systems that support ecological nutrient management is an important component of achieving environmental justice and agroecological resilience, and sustainable production systems.

Our objectives were to determine the responses of plants and soil to organic matter amendments derived from human excreta and to estimate the potential for the recycling of human excreta to meet country-level crop nutrient demands. Specifically, we compared the effects of composted human feces on soil and plant processes to two other human waste products (biosolids and biofertilizer), inorganic fertilization, and an un-amended control. We hypothesized that the application of composted feces to soil would increase crop production, due to the presence of a suite of macro- and micronutrients. We predicted that the boost in crop production would carry-over in time due to slow mineralization of nutrients and improvements in soil health. We further hypothesized these improvements in soil health would lead to lower aqueous and gaseous nutrient losses. We also provide an estimate of the potential for circular sanitation to meet Haiti's crop N, P, and K demands, along with an assessment of hurdles to widespread adoption of circular sanitation-agriculture systems.

MATERIALS AND METHODS

Experimental Design

We conducted the experiment in a climate-controlled greenhouse at Pope Greenhouse facilities at the University of Hawaii at Mānoa from August 2017 through April 2018. Daily mean temperature was 27.6°C and mean relative humidity was 69.6% over the course of the experiment. Soil used for the experiment was weathered from basic igneous rock with silty clay texture and classified as very-fine, kaolinitic, isohyperthermic Rhodic Eutrustox in the Lahaina series. Soil was collected from the 0 to 30 cm depth of an uncultivated field directly adjacent to an organic agricultural system on Oahu, Hawaii (21.555°N, 158.117°W). The field was previously used for irrigated sugarcane production and had been fallowed for at least 10 years prior to this study. Soil was sieved to 2 mm and mixed well prior to distributing it into growth pots. Each growth pot consisted of a 7.5 L bucket (diameter = 25 cm) perforated for drainage. The base of the pot was layered with a 20 µm Whatman #4 filter followed by 3.5 mm of HCl-rinsed silica sand and 3.5 kg of sieved soil. Each pot was nested inside a second 7.5 L bucket so that leachate could be collected and analyzed for nutrient content.

Potted soils were amended with compost derived from human feces and compared with four other treatments, including biosolids, liquid biofertilizer, urea (46-0-0 N-P-K), and an unfertilized control ($n = 3$). The compost amendment was generated by SOIL (Kramer et al., 2011), a non-governmental organization that provides ecological-based sanitation services to households and communities in Cap Haïtien, Haiti. SOIL's EcoSan system deploys 20 L container-based, urine-diverting toilets to separate solid (feces) and liquid (urine) waste. Urine is captured in a 4 L plastic container and is disposed of on-site, ideally on a pervious surface, by toilet users. Sugarcane bagasse is used as cover on solid waste after each use. Solid material is collected on a weekly basis and transported to a centralized composting facility where sugarcane bagasse is again used as lining (30 cm on the base of the pile) and cover material (10 cm on top of the pile), resulting in a bagasse-to-feces ratio of 2:1. An aerobic, thermophilic composting process is used to sanitize feces and produce a nutrient-rich soil amendment (Kramer et al., 2011; Ryals et al., 2019). Compost pile temperatures and *E. coli* concentration are regularly monitoring during the composting process to ensure that thermophilic conditions are achieved. The biosolids amendment was a Class A commercial-grade fertilizer derived from municipal solid waste that has undergone anaerobic digestion, centrifuge dewatering, heat drying and pelletization and was collected from the Honolulu Sand Island Wastewater Treatment Plant (R.M. Towill Corporation, 2017). The liquid biofertilizer amendment was produced from a wastewater treatment facility that uses anaerobic digestion and thermal hydrolysis to produce a pathogen-free liquid biofertilizer (Lystegro, Lystek, Canada). Urea was used as a comparison in this study because it is a widely used synthetic N-based fertilizer. Global production of urea has increased by 25% in the past decade, which outpaces the growth of other N-based fertilizers (e.g., ammonium nitrate; IFASTAT, 2021). All pots were arranged in a randomized block configuration to minimize the effects of microclimate variability within the greenhouse.

All treatments were applied one-time only and immediately prior to the first planting. The application rate for all treatments except for the control was equivalent to 100 kg potentially available N ha^{-1}, which is an intermediate N application rate for the radish crop used in this study, *Raphanus raphanistrum sativus* (Fox and Valenzuela, 1996; Jawad et al., 2015; Yuan et al., 2015). Plant available nitrogen (PAN) was calculated for each amendment using the following equation:

$$\mathrm{PAN} = \mathrm{NH_4 - N} + [\mathrm{NO_3 - N} + \mathrm{NO_2 - N}] + \mathrm{K_{min}}\,(\mathrm{Org - N})$$

where K_{min} equals mineralizable N. The N mineralization rate of EcoSan compost was estimated at 7% based on the average value of 16 studies measuring N mineralization in composted biosolids between 1977 and 2011 (Rigby et al., 2016). The N mineralization rate of 20% was estimated for the biosolids treatment based on the EPA's recommended rate for anaerobically digested biosolids (United States Environmental Protection Agency, 1995). The N mineralization rate of 40% was provided by the manufacturer for the liquid biofertilizer treatment (Lystek Inc, 2017). All N was considered available for urea, which consists of 46% N. The treatments were added into the pots and incorporated into the soil manually prior to seed planting. Initial soil organic C and total N concentrations and contents and Treatment C, PAN, and total N application amounts are presented in **Table 1**.

Crop Biomass and Nutrient Content

Nine radish (*Raphanus raphanistrum sativus*) seeds were sown in each pot, thinned to the three strongest seedlings after 7 days, and harvested after 36 days. Radish was selected for this experiment because of its fast growth rate and time to maturation. Six consecutive crops of radishes were planted in each pot without reapplication of organic amendments or fertilizer. At the end of each crop cycle, radishes were carefully uprooted, washed with deionized water, and divided at the crown to separate above- and belowground plant components. Plant samples were dried at 65°C until a stable dry weight was achieved. Fresh and dry biomass for the above- and belowground components were recorded for all six crop cycles. A subsample of aboveground biomass from each pot after the first two crop cycles was composited and analyzed for macro and micronutrient concentrations at the University of Hawaii Hilo Analytical Laboratory. Calcium (Ca), Potassium (K), Magnesium (Mg), Sodium (Na), Phosphorus (P), Arsenic (As), Copper (Cu), Iron (Fe), Manganese (Mn), Lead (Pb), and Zinc (Zn) concentrations were measured on a Varian Vista-MPX CCD ICP-OES at the University of Hawaii (UH) at Hilo Analytical Laboratory according to the methods described by Zimmermann (2000). Brielfy, samples were dried at 55°C, ground finely, and dry-ashed in a muffle furnace at 500°C. Ash residue is dissolved in 1 M hydrochloric acid prior to analysis on the ICP-OES. Chloride (Cl) concentrations were measured on a Lachat Quickchem 8,500

TABLE 1 | Carbon and N concentrations and contents of soil and amendments.

	% C	C content (g pot^{-1})	% N	N content (g pot^{-1})	
Initial Soil	2.24	78.4	0.19	6.65	
Amendment Type	**% C**	**C added (g pot^{-1})**	**% N**	**PAN added (g pot^{-1})**	**Total N added (g pot^{-1})**
Urea	20.0	0.20	46.0	0.45	0.45
Compost	24.7	53.2	3.00	0.45	6.46
Biosolids	37.6	20.0	4.26	0.45	2.26
Biofertilizer	2.24	3.00	5.29	0.45	0.61

Amendment application was based on a rate of 100 kg of potentially available N (PAN) ha^{-1}, leading to differences in amounts of total N and C applied among treatments.

Series 2 according to the methods described by Jones (2001). Plant nutrient concentrations were multiplied by biomass to calculate nutrient content.

Soil Carbon and Nutrients

Soil organic C and total N concentrations were analyzed immediately after treatment application, and at the end of crop cycles 1, 2, and 6. A subsample of soil was air-dried, ground to a fine powder using a mortar and pestle and analyzed for soil total C and N concentrations on Costech 4,100 Elemental Analyzer at the University of Hawaii at Hilo Analytical Laboratory. Concentrations of exchangeable cations, including calcium (Ca^{2+}), magnesium (Mg^{2+}), potassium (K^{+}) and sodium (Na^{+}), were measured initially and at the end of crop cycle 6 using the ammonium acetate method buffered at pH 7.0 (Lavkulich, 1971) and analyzed on a Thermo iCAP DUO 7,400 ICP-OES at the UH Hilo Analytical Laboratory. Cation exchange capacity was calculated as the sum of base cations. Soils were also analyzed for pH using a slurry method with a 1 to 2 ratio of soil:deionized water.

Soil extractable N [nitrate (NO_3^-) + nitrite (NO_2^+) and ammonium (NH_4^+)] was measured at five timepoints: immediately after treatment application, and at weeks 3, 6, 9, and 12 of the study. These timepoints are related to the beginning, middle, and end of the first two crop cycles. Three soil cores (1 cm diameter × 10 cm deep) were collected from each pot about 2.5 cm from each radish taproot. To determine amounts of extractable N, 6 g of soil was mixed with 30 mL of 2M KCl, shaken for 60 min on an orbital shaker, and filtered with a Whatman #1 filter. The filtrate was collected, stored in a −20°C freezer, and shipped on dry ice to the University of Hawaii at Hilo Analytical Laboratory for colorimetric analysis on a Lachat Quickchem 8,500 Series 2 (Zimmermann, 1997).

Water and Nutrient Leaching

All pots were watered to field capacity (3,000 mL deionized water to 3.5 kg soil) immediately prior to treatment application. Each pot was watered daily with the same amount of deionized water as needed, typically 100 mL, to maintain approximate field capacity. Excess water equivalent to a 1.85 cm stimulated rainfall event was added approximately weekly to induce leaching events and create variable soil water conditions present in field settings. Leachate was collected 24 h after excess watering events on days 2, 3, 9, 22, 39, 47, 51, 71, 74, 116, 152, and 192, which include four events during the first two crop cycles and events during the fallow period after subsequent crop cycles. The total volume of leachate was recorded for each pot and a 50 mL subsample was collected and stored in at −20 °C. Leachate samples from the first two crop cycles were also analyzed for NO_3^-, NH^{4+}, and phosphate (PO_4^{3-}) concentrations. Inorganic N and P in leachate was not measured after the second crop cycle, when concentrations remained below the detection limit of the analyzer.

Concentrations of NO_3^- and NH^{4+} in each leachate sample were measured by reduction to nitrite and reaction with Griess reagent and the indophenol blue method of reflectometric determination, respectively, using a Reflectoquant (EMD Millipore Corporation; Billerica, MA USA). Lower limits for nutrient detection were < 3 mg for NO_3^- and < 0.2 mg for NH^{4+}. The total mass of N leached in each form was then calculated by multiplying the concentration of NO_3-N and NH_4-N in each leachate subsample by the total volume of leachate collected during the leaching event. The total mass of N leached from each pot was then calculated by summing the mass of N lost during each leaching event. We then calculated the mean percent N lost *via* leaching for each treatment group as a function of the amount of total N added to each pot, which varied by treatment since PAN was kept constant.

The concentration of PO_4^{3-} in leachate samples was measured using the phosphomolybdenum blue method of reflectometric determination using a Reflectoquant (EMD Millipore Corporation; Billerica, MA USA). Lower limits for nutrient detection were <5 ppb. The total mass of P leached as PO_4^{3-} was then calculated by multiplying the concentration of PO_4-P in each leachate subsample by the total volume of leachate collected during the leaching event. The total mass of phosphorus leached as PO_4^{3-} from each pot was calculated by summing the mass of phosphorus lost during each leaching event.

Greenhouse Gas Emissions

Soil greenhouse gas fluxes were measured prior to and immediately following treatment application and twice per week during the first two cropping cycles. When moisture is held relatively constant, soil greenhouse gas fluxes tend to be highest for the first few days to weeks following application of amendments or fertilizer (Ryals and Silver, 2013). Greenhouse gas fluxes were no longer measured after the second crop cycle, when there were no longer treatment differences observed. Vented static flux chambers (7.5 L) were fitted on top of the growth pots, and 30 mL gas samples were collected from the chamber headspace at 0, 5, 10, 20, and 30-min time points. Gas samples were immediately transferred to 20 mL evacuated glass vials (Wheaton) with a butyl rubber stopper (GeoMicrobial Technologies) and sealed with an aluminum crimp. Samples were analyzed for concentrations of carbon dioxide (CO_2), nitrous oxide (N_2O), and methane (CH_4) on a gas chromatograph outfitted with a thermal conductivity detector, electron capture detector, and flame ionization detector (Shimanzu Analyzer 5,000-A, University of California, Merced). Fluxes were calculated using an iterative exponential curve-fitting approach (Matthias et al., 1978). We summed daily values using linear interpolation between sampling time points to estimate cumulative soil greenhouse emissions over each of the two crop cycles.

Potential for Ecological Sanitation to Meet Crop Nutrient Demands in Haiti

We used available data on crop biomass, crop nutrient demand, and the production of human excreta in Haiti to demonstrate the relevance of EcoSan at scale. We estimated the potential contribution of excreta-derived nutrients to meet annual crop N, P, and K demands in Haiti. Crop nutrient demand was calculated by multiplying the average production from 2017 to 2019 of FAOSTAT-reported crops in Haiti by crop-specific nutrient removal (Roy et al., 2006; FAOSTAT Statistical Database, 2021). Sisal, yam, melon, and chicory root were excluded because adequate removal values were not found. Crops that are grown in Haiti but not included in the FAOSTAT database were excluded from this analysis. Urine and fecal nutrients were calculated using Haiti-specific values in Jönsson et al. (2005) and an estimated Haitian population of 11.26 million. The maximum potential percentage demand met by supply assumed 100% of nutrients embedded in excreta could be recovered. We recognize that this accounts for neither the nutrient losses that occur during the composting process or urine recovery, nor the potential increases in nutrient retention or nutrient use efficiency with elevated soil organic matter. We also considered barriers to widespread adoption of EcoSan and recommend pathways to overcome these barriers.

Statistical Analysis

One-way analyses of variance (ANOVA) were used to determine significant differences in each parameter measured between treatment groups for each crop round. Analyses included a blocking effect to account for potential spatial variation in greenhouse conditions. When the results of the ANOVA indicated a significant difference between means ($p < 0.05$), a Tukey *Post-Hoc* Test was conducted to determine differences between specific treatment groups. To assess the changes over time, we used repeated measures multivariate analysis of variance (MANOVA) with aboveground biomass, belowground biomass, total biomass, and soil extractable N as response variables and treatment, time, and treatment × time interactions as model effect factors. Statistical tests were performed using JMP Pro 14.2 (SAS Institute Inc, 1989). Variables that were not normally distributed were log transformed to meet assumptions for ANOVA and MANOVA. Data are reported as mean values followed by ± standard error. Statistical significance was determined as $p < 0.05$.

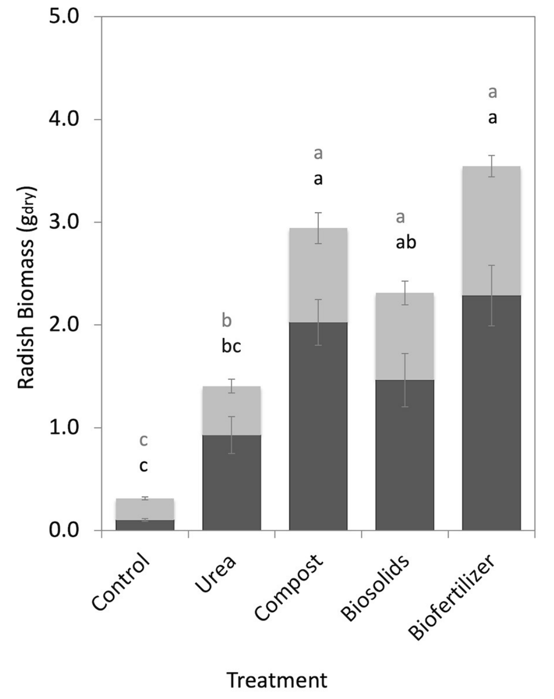

FIGURE 1 | Total plant biomass of the first crop of radishes grown in pots with soils with amendments derived from human excreta, compared to a synthetic N-based fertilizer (urea) and an unamended/unfertilized control. Light bars represent treatment means of dry aboveground biomass, and dark bars represent treatment means of dry belowground biomass. Error bars indicate ± standard error for each biomass component. Differences in lightly shaded letters indicate significant treatment differences for aboveground biomass, whereas darker letter indicate treatment difference of belowground biomass, as determined by an ANOVA and post hoc Tukey means comparison test with significance determined as $p < 0.05$.

RESULTS

Crop Biomass and Nutrient Content

There was a significant treatment effect on crop production after the first crop cycle ($p < 0.0001$; **Figure 1**). The strongest total plant biomass response was observed with the human waste amendments, which was more than two-fold greater than urea fertilization ($p < 0.0001$) and ten-fold greater than the control ($p < 0.0001$). Treatment differences among human waste amendments were not statistically significant and ranged from 2.3 to 3.5 g_{dry}. Urea increased plant biomass compared to control ($p < 0.0001$). Treatment effects were similar for both above- and belowground plant components, and the block effect was not significant.

Plant biomass responses to treatment diverged over time following the one-time application (**Figure 2**). There were significant treatment differences for aboveground, belowground, and total plant biomass through time over the course of all

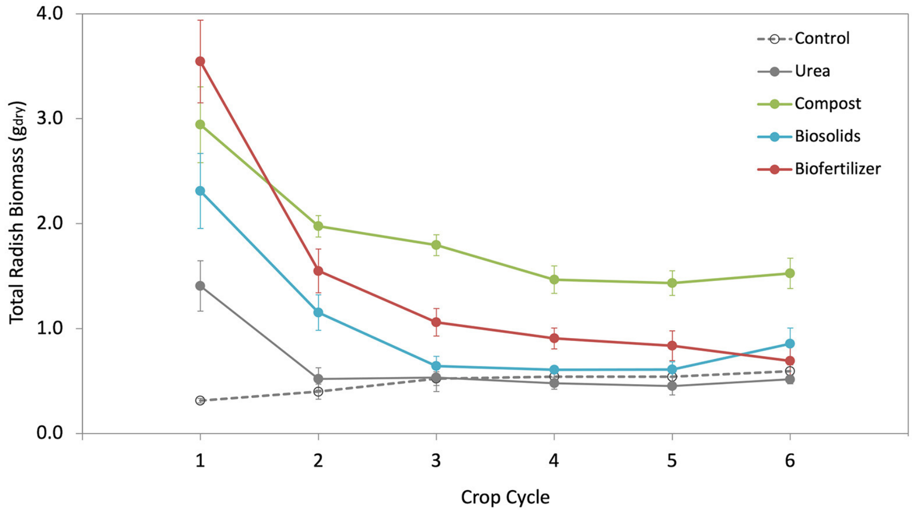

FIGURE 2 | Total plant biomass of six consecutive radish crop cycles. Treatments were added only one-time, prior to planting seeds in the first crop cycle. Symbols represent treatment means at the time of harvest, with ± standard error bars.

six consecutive crop cycles ($p < 0.0001$). There was also a significant block effect for aboveground biomass ($p = 0.004$) and a significant interaction between time and treatment ($p < 0.001$) for all plant biomass measurements. Urea did not significantly increase plant biomass relative to the control beyond the first crop cycle. The human waste amendments differed in the duration of their carry-over effect on plant biomass. Biosolids increased total plant biomass relative to control for the first two crop cycles, while Biofertilizer had an effect for the first three crop cycles. In contrast, Compost significantly increased plant biomass throughout all six crop cycles, and remained 2–3 times greater than all other treatments at the end of the experiment. Over the course of six crop cycles, cumulative plant biomass from human waste amended soils ranged from 6.2 ± 0.4 g_{dry} (Biosolids) to 11.1 ± 0.5 g_{dry} (Compost), while it was only 3.9 ± 0.3 g_{dry} for Urea and 2.9 ± 0.1 g_{dry} for Control.

Plant tissue nutrient concentrations did not differ greatly among treatments, although some differences were observed (**Supplementary Table 1**). Compost increased N concentration in leaves by 35% compared to all other treatments in the first crop cycle ($p = 0.007$), but this effect did not carry-over to the next crop cycle ($p = 0.25$). Leaf tissue Na concentrations of all amendment treatments were significantly greater than control, but only the Biofertilizer treatment was significantly greater than crop fertilized with urea. In the first crop cycle, leaf Cl tissue was highest for Biosolids ($p < 0.001$), but no significant difference was detected in the second crop cycle. There were no significant treatment effects in Ca, K, Mg, P, As, Cu, Fe, Mn, Pb, or Zn leaf concentrations.

Soil Organic Carbon and Nutrients

There was no significant difference in total C or N concentrations of the potted soil immediately after treatment application (Day 1; $p = 0.43$ for %N, $p = 0.30$ for %C). However, at the end of the first crop cycle (Day 37), we detected a significant treatment effect on soil organic C concentration ($p = 0.0011$). Compost amended soils had a significantly higher soil organic C concentration (2.48 ± 0.04 %C) than the four other treatments. Soil organic C concentrations of the remaining treatments were not significantly different from the control, which was 2.04 ± 0.05 %C. At the end of six consecutive crop cycles (Day 239), both soil organic C and total N were significantly greater in Compost than all other treatments (**Figure 3**). Mean soil organic C concentration in Compost was 37% greater and soil total N concentration was 29% greater compared to other treatments. Soil organic C concentration in compost increased linearly through time ($R^2 = 0.93$).

Soil inorganic N pools decreased significantly through time ($p < 0.001$), with a significant treatment effect ($p = 0.019$) and treatment and time interaction ($p = 0.024$). Initial inorganic N pools were approximately two times greater for soils amended with Biosolids and four times greater for soils amended with Biofertilizer, compared to Control. This trend was driven primarily by higher amounts of extractable NH_4^+ upon application of these amendments. By the end of the first crop cycle (Day 36), soil inorganic N pools were very low, and not significantly influenced by treatment. Compost and Biosolids amended soils experienced a small pulse in soil extractable N at the mid-point of the second crop cycle, which again subsided by the end of that cycle (**Figure 4**).

Cation exchange capacity did not differ significant across treatments at the end of the experiment ($p = 0.29$; **Table 2**). Base saturation was dominated by calcium (mean 88 ± 0.7% of total CEC) across all treatments. Extractable K^+ concentrations were significantly higher than all other treatments (ANOVA p-value $= 0.0003$; Tukey p-values < 0.005). The urea, biosolids, and biofertilizer treatments had an average of 56% less extractable K^+ relative to the control by the end of the experiment. In contrast, the compost treatment had 190% more extractable K^+ relative to the control. The compost treatment also had significantly higher concentrations of extractable Mg^+ and Na^+ compared to the control, urea, and biofertilizer treatments (**Table 2**). Soil pH averaged 7.83 ± 0.03 across all treatments, and there were no significant differences in soil pH among treatments or through time.

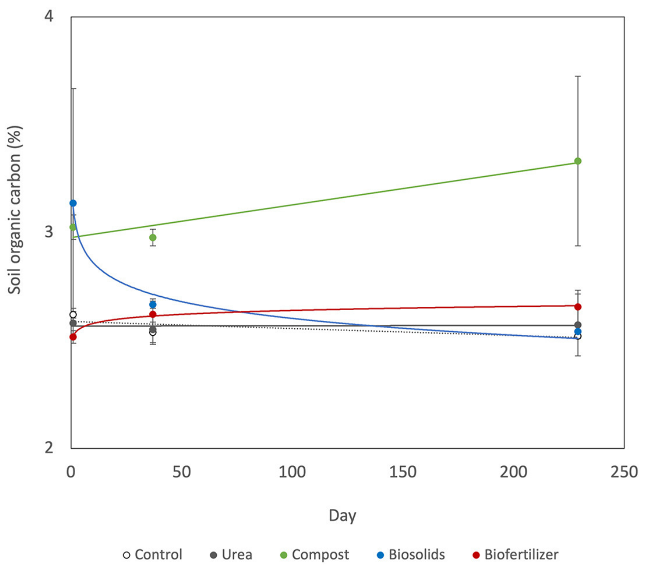

FIGURE 3 | Percent soil organic carbon immediately after adding amendments (Day 1), after the first crop cycle (Day 37), and after the sixth crop cycle (Day 239).

Water and Nutrient Leaching

The amount of water leached from the pots during the first crop cycle varied from 10 to 17% of total amount of water added, and there was a significant treatment effect ($p = 0.006$). Compost leached significantly less water than Control, Urea, and Biofertilizer ($p < 0.05$), and marginally significantly less than Biosolids ($p = 0.10$). The amount of water leached from Biosolids was significantly less than Control. By the end of the sixth crop cycle, the treatment effect on water loss *via* leaching was considerably stronger compared to the first crop cycle with similar trends (**Figure 5**). Relative to the amount of water added, 7 and 10% of water was lost *via* leaching from Compost and Biosolids, respectively. Compost leached 2.4 and 3.2 times less water than the Urea and Control, respectively. There was not a significant difference in water leached between Biofertilizer, Urea, and Control.

Inorganic N ($NO_3^- + NH_4^+$) leaching rates were highest at the beginning of the experiment following treatment application, with NO_3^- contributing between 80 and 99% of total inorganic N leached across all treatments. During the first crop cycle, the amount of NH_4^+ leached was highest for Urea, whereas the amount of NO_3^- leached was highest for Compost. Approximately 93% of NO_3^- leached from compost occurred within the first three weeks, leading to a total of 709 ± 169 mg NO_3^-N leached from Compost. This amount was an order of magnitude higher than Urea, which had the second highest NO_3^- leaching. There were no significant treatment differences after Day 21. By the second crop cycle (beginning Day 39), dynamics of N leaching changed dramatically, reducing from an average across all treatments of 148 mg NO_3^--N in crop cycle 1 to 1.9 mg NO_3^--N in crop cycle 2. Similarly, the amount of NH_4^+-N that leached was reduced from an average of 5.6 to 0.09 mg NH_4^+-N in crop cycles 1 and 2, respectively. There was a significant

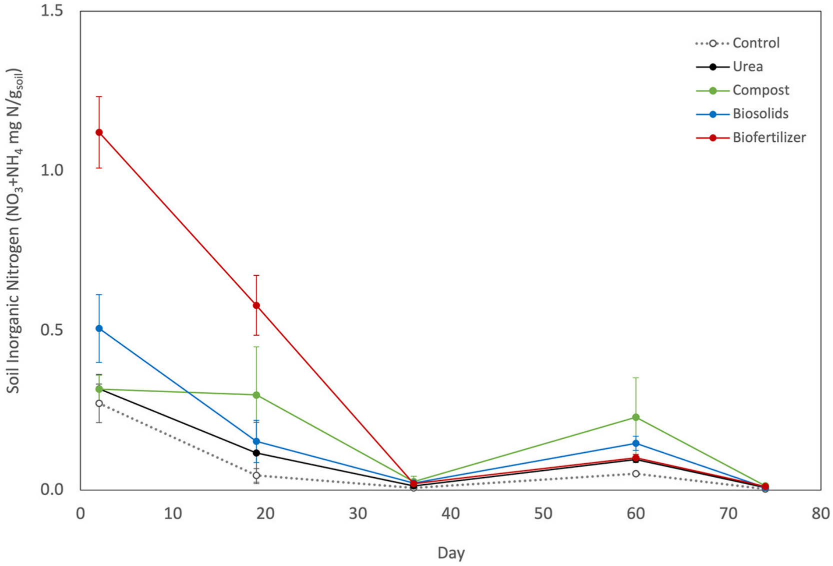

FIGURE 4 | Soil total inorganic N ($NO_3 + NH_4$) pools within the first two crop cycles.

TABLE 2 | Soil pH, extractable nutrients, and cation exchange capacity (CEC) after the sixth crop cycle.

Treatment	soil pH	Ca^{2+}	K^{+}	Mg^{2+}	Na^{+}	CEC
		$(cmol^{+}\ kg^{-1})$				
Control	7.8 ± 0.04	23.4 ± 0.58	0.11 ± 0.006^{b}	2.32 ± 0.05^{b}	0.27 ± 0.011^{b}	26.1 ± 0.58
Urea	7.8 ± 0.03	23.1 ± 0.80	0.09 ± 0.014^{b}	2.34 ± 0.10^{b}	0.27 ± 0.011^{b}	25.8 ± 0.81
Compost	7.8 ± 0.03	22.0 ± 0.71	0.31 ± 0.075^{a}	2.80 ± 0.08^{a}	0.48 ± 0.036^{b}	25.6 ± 0.72
Biosolids	7.7 ± 0.04	22.9 ± 0.33	0.02 ± 0.013^{b}	2.45 ± 0.11^{ab}	0.43 ± 0.029^{b}	25.8 ± 0.35
Biofertilizer	7.9 ± 0.14	21.0 ± 0.80	0.03 ± 0.014^{b}	2.17 ± 0.05^{b}	0.21 ± 0.017^{b}	23.4 ± 1.42

Letters indicate significance at $p < 0.05$.

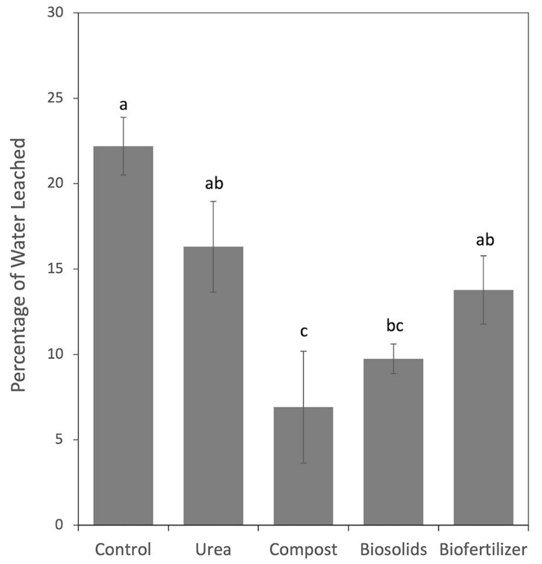

FIGURE 5 | Cumulative water lost *via* leaching as a percentage of cumulative water applied. Bars represent treatment means. Error bars indicate ± standard error. Letters indicate significant treatment differences as determined by an ANOVA and post hoc Tukey means comparison test with significance determined as $p < 0.05$.

treatment difference in cumulative N leaching ($p = 0.0069$). The Urea treatment lost significantly more N *via* leaching (20% of total N added) than the Biosolids treatment (0.5% of total N added; $p = 0.0044$). Cumulative N leaching from the Compost treatment (11% of total N added) and the Biofertilizer treatment (8% of total N added) was not significantly different from Urea. We did not detect PO_4^{3-} leaching from any of the treatments.

Soil Greenhouse Gas Emissions

There were no significant treatment differences in soil CO_2 fluxes through time or in cumulative CO_2 efflux from potted soils (**Figure 6A**). Fluxes of CH_4 were negligible or low throughout the experiment. There were no significant treatment differences in cumulative soil CH_4 flux (**Figure 6B**). Fluxes of N_2O were greatest within the first two weeks of the experiment. There was a significant treatment difference in cumulative soil N_2O flux ($p < 0.0001$). Biosolids cumulative soil N_2O flux was significantly greater than all other treatments (**Figure 6C**). Soil N_2O emissions factors ranged from 0.03 ± 0.01 (Compost) to 4.5 ± 0.6 (Biosolids). There was a significant treatment difference in soil N_2O emissions factors ($p = 0.0005$). The emissions factor for Biosolids was significantly higher than all other treatments ($p < 0.008$), except Biofertilizer ($p = 0.25$). Compost soil N_2O emissions factor was significantly less than Biosolids ($p = 0.0004$) and Biofertilizer ($p = 0.004$) and marginally significant compared to Urea ($p = 0.10$).

The fate of total added N was summarized in a partial N mass balance (**Figure 7**). We calculated a partial N mass balance based on the amount of measured N losses from treatments relative to the unfertilized control, including inorganic N leaching, N_2O–N, and plant N uptake. Nitrogen losses accounted for from the Compost treatment exceeded the amount of N added in units of PAN, largely due to initial NO_3 leaching losses. The highest proportion of unaccounted N losses (76% of PAN added) was from the Urea treatment, while 20 and 56% of PAN added in Biosolids and Biofertilizer treatments were unaccounted for. We also observed increases in soil total N in the Compost and Biofertilizer treatments which were greater than cumulative N losses. In contrast, soil total N from the Urea treatment declined slightly over time relative to the control.

Potential for Ecological Sanitation to Meet Crop Nutrient Demands in Haiti

Average annual crop production (2017–2019) of 24 FAOSTAT crop types in Haiti was 3.4 MMt yr^{-1} (**Supplementary Table 2**). Five crops—sugar cane, mangoes, bananas, avocados, and rice—contributed nearly 85% of total annual crop production. Total N, P, and K demand from annual crop production is presented in **Table 3**. The capture and transformation of human excreta *via* composting recovery could potentially supply 13, 22, and 11% of crop N, P, and K (**Table 3**), assuming 100% nutrient recovery. Urine, which is currently disposed of on-site in SOIL's sanitation system but also has the potential for nutrient recovery, could meet an even greater amount of crop nutrient demand, potentially up to 83, 44, and 32% of N, P, and K. Several ecological, technical, and sociocultural barriers impede the widespread adoption of coupled sanitation-agriculture systems (**Table 4**).

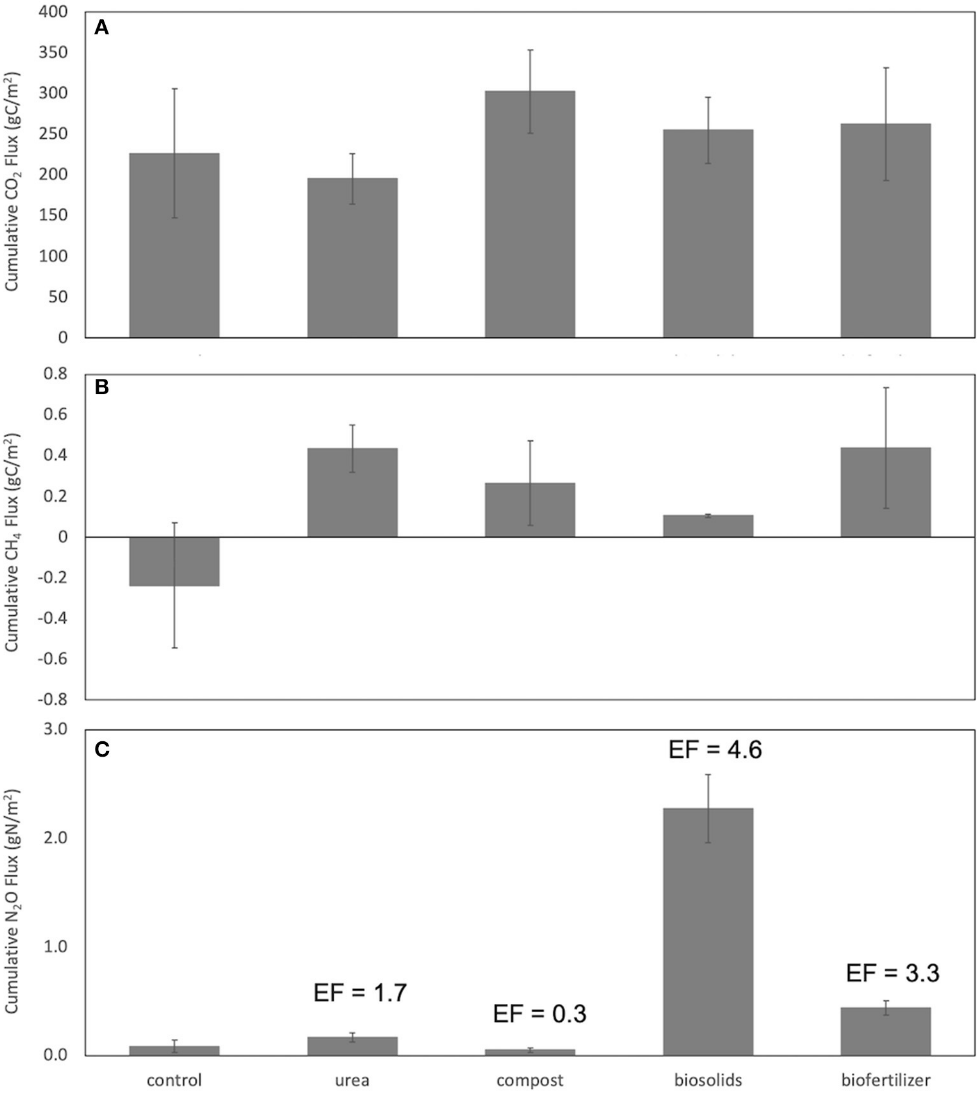

FIGURE 6 | Cumulative soil emissions of **(A)** CO_2, **(B)** CH_4, and **(C)** N_2O during the first two crop cycles from days 1 through 73. Bars represent treatment means. Error bars indicate ± standard error. EF indicates treatment N_2O emissions factors, calculated as the percent of total N added lost as gaseous N_2O.

DISCUSSION

Crop and Soil Responses to Human Waste Amendments

We measured the response of plant production to a one-time application of three human excreta-derived soil amendments: compost from container-based EcoSan, pelletized biosolids from wastewater treatment, and biofertilizer from thermal hydrolysis after wastewater treatment. In the first crop cycle, all three excreta-derived amendments increased plant production significantly relative to urea-fertilized and unfertilized control soils. These results align with short-term greenhouse and field studies of excreta-derived amendments (e.g., Sumner, 2000; Elliott and O'Connor, 2007; Moya et al., 2019a; Brown et al., 2020).

The agronomic effects of biosolids have been well studied in the context of urban waste management (Brown et al., 2020). Sustained increases in crop yields, reduction in N fertilizer requirements, and increases in soil organic matter have been observed with the application of biosolids to vegetable production systems and urban gardens across a range of soil types and climates (e.g., Ozores-Hampton and Peach, 2002; Alvarez-Campos and Evanylo, 2019). Residues from wastewater treatment can also be treated further with thermal hydrolysis to produce liquid biofertilizers that are rich in mineral N and beneficial microorganisms. Liquid biofertilizers have been less extensively studied relative to biosolids, and little information is available on the effects of soil nutrient cycling and loss associated with their application. Recent studies indicate similar positive benefits to plant production (Badewa and Oelbermann, 2020; de Matos

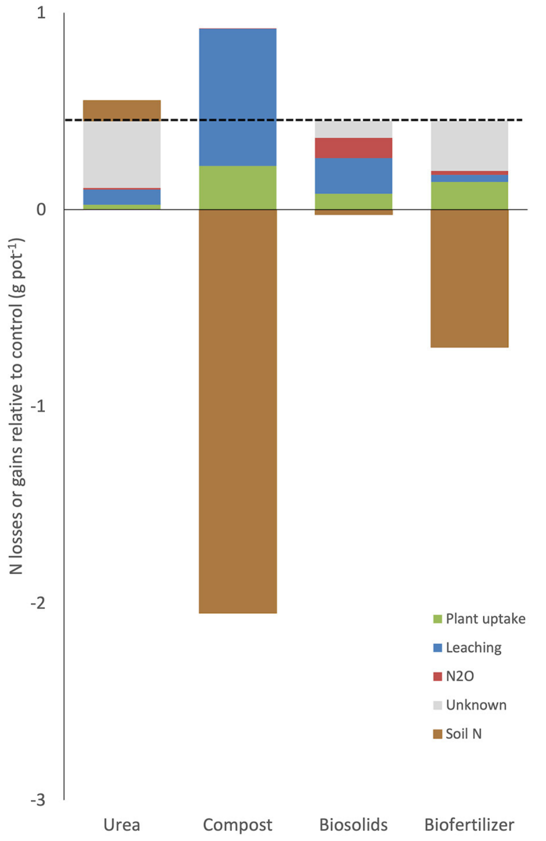

FIGURE 7 | A partial N mass balance illustrating the losses of added PAN from pots in the forms of plant N uptake (green), N_2O–N emissions (red), and inorganic N leached (blue). Nitrogen mass loss from each of these pathways was determined as treatment minus control to account for plant and microbial use of N without amendments or fertilizer. Gray bars indicated unknown losses of N, which may include N_2 or other forms of reactive N. The black dotted line indicates the amount of PAN added to each pot. Brown bars represent. Brown bars represent treatment differences (treatment—control) in soil total N. Positive values indicate fluxes to the environment, whereas negative values indicate N sinks in the pots.

Nascimento et al., 2020). Our results corroborate existing studies on the agronomic benefits of biosolids and biofertilizer, and provide new information on the longevity of these responses across crop cycles.

There are few experiments testing the effect of EcoSan compost on plant production and soil nutrient cycling processes. EcoSan compost has been shown to increase yields of banana (Jothimani et al., 2013), maize (Krause et al., 2016), marigold (Jothimani and Sangeetha, 2012), cauliflower (Sharda and Shinjo, 2020), and lettuce (Schröder et al., 2021) relative to standard fertilization practices in the given contexts. There is a paucity of data on the effects of EcoSan compost on soil physiochemical properties and nutrient losses. We found that, while EcoSan compost did not significantly alter soil CEC, it did increase the concentrations of exchangeable K^+ and Mg^{2+} in a soil with deficient levels of these macronutrients. While tissue K^+ and Mg^{2+}concentrations of radishes grown in soils blended with EcoSan compost were not significantly higher than those of other treatments, alleviation of these macronutrient deficiencies likely contributed to greater biomass. A field experiment comparing EcoSan manure to a mineral fertilizer in cauliflower production systems also observed increases in crop production and plant uptake of N, P, and K (Sharda and Shinjo, 2020).

Only a handful of studies exist that conduct a nutrient mass balance in the agricultural use of EcoSan compost (e.g., Krause and Rotter, 2018; Schröder et al., 2021). The effects of EcoSan compost on water infiltration, nutrient leaching, or greenhouse gas emissions are similarly poorly studied. Our study provides some of the first observations of these parameters in soils treated with EcoSan and can be used to inform future research. Extrapolation of observations from pot studies can be useful for building conceptual models and predicting treatment effects, but field experiments are necessary for furthering understanding of plant-soil feedbacks (Forero et al., 2019). Additional studies are needed in field contexts, across multiple climate and edaphic conditions, and through time to refine our understanding of the fate and transport of recycled nutrients in EcoSan systems. In our greenhouse experiment, we detected treatment differences in N loss pathways as a function of N applied and compared to an unfertilized control. This approach assumes that measured N losses were derived from the fertilizer or organic amendments. However, the addition of fertilizers or organic matter amendments to a soil can induce positive or negative priming effects, thereby changing rates of C and N mineralization of soil organic matter that are non-additive (Jenkinson et al., 1985; Kuzyakov et al., 2000). Field studies using stable isotopes of ^{15}N and ^{13}C can be used to quantify the direction and magnitude of potential priming effects, improve our understanding of the fate of added nutrients, and clarify the nutrient use efficiency of these novel organic amendments (Gardner and Drinkwater, 2009; Lerch et al., 2019).

Our results, combined with a handful of other available studies, suggest that nutrients in human excreta-derived amendments provide a viable substitute for mineral fertilizers by building soil organic C and promoting internal nutrient cycling. Maintaining or increasing soil organic C is a central principle of ecological nutrient management because of its role in the biological, physical, and chemical functions of soil (Reeves, 1997; Tully and Ryals, 2017). We found the EcoSan compost has the potential to increase soil organic C content, and numerous studies have reported the carbon sequestration potential of compost derived from other feedstocks (e.g., (Ryals et al., 2014; Mar Montiel-Rozas et al., 2016; Tautges et al., 2019) even when considering life cycle greenhouse gas emissions (DeLonge et al., 2013; Martínez-Blanco et al., 2013). Our observed carry-over impact on plant production with EcoSan compost suggests improved internal nutrient cycling. The timeframe for which EcoSan compost can continue to supply nutrients after application remains an important question that could inform best management practices for application amount and frequency through time. Higher rates or frequency of EcoSan compost may be needed early on while soil organic matter is accruing, however application rates could potential decrease as internal nutrient cycling processes are enhanced through time. This

TABLE 3 | Estimated potential contribution of excreta-derived nutrients to meet crop N, P, and K demand in Haiti.

Nutrient	Crop Nutrient Demand (Mt/y)	Fecal Nutrients (Mt/y)	Urine Nutrients (Mt/y)	Potential Annual Nutrient Demand Met by Feces (%)	Potential Annual Nutrient Demand Met by Urine (%)	Potential Annual Nutrient Demand Met by Excreta (%)
Nitrogen (N)	25671	3378	21394	13	83	96
Phosphorus (P)	5094	1126	2252	22	44	66
Potassium (K)	31681	3378	10134	11	32	43

Crop nutrient demand was calculated by multiplying the average production from 2017–2019 of FAOSTAT-reported crops in Haiti by crop-specific nutrient removal (Roy et al., 2006; FAO, 2021, ***Supplementary Table 1****). Feces and urine nutrient supplies were calculated using Haiti-specific values in Kramer et al. (2011) and an estimated Haitian population of 11.26 million. Maximum potential percentage demand met by supply assumed 100% of nutrients embedded in excreta could be recovered.*

TABLE 4 | Barriers to adoption of EcoSan and recommendations to overcome barriers.

Type of Barrier	Recommendations
1. Ecological barriers	
Source of agricultural waste for composting process	Conduct agroecological and economic analyses of regional organic waste streams
Effective compost application to agricultural lands	Scientific studies on benefits, trade-offs, and optimal application rates based on site and crop conditions; Local agricultural extension and technical assistance resources
Climate change and extreme weather events	Climate resilient sanitation infrastructure; Analysis and demonstration of agroecosystem resilience to climate change impacts with EcoSan compost
2. Institutional and technical barriers	
Lack of infrastructure and/or transformation of existing infrastructure	Long-term investment in EcoSan systems; Shared collective knowledge from EcoSan services around the world
Compost transportation	Decentralized compost sites to reduce transport distances; Partnerships with other logistics businesses to capture economies of scale
Worker health risks	Microbial health risk assessment associated with all stages of EcoSan; Safety guidance and oversight for sanitation workers and farm workers
Urine is difficult to transport	Couple nutrient recapture from urine to feces management system (e.g., use biochar filter in toilet to adsorb urine nutrients or from communal urine soak pits)
3. Cultural barriers	
Poop is taboo and fears about using fertilizer derived from human excreta	Elevate the urgency of SDG 6 and its intersection with other SDGs; Education about safe excreta treatment; Scientific research on the safety of EcoSan and compost use
"Pipe" dream	Shift the culture of sewered sanitation as the most evolved service; Design sanitation systems based on natural resource constraints
Familiarity and reliance on chemical fertilizers	Promotion and financial support for soil health practices; Science and education about long term benefits of compost use
Insecure land ownership	Increase the capacity for farmers to formally own land

Barriers were identified based on literature reviews as discussed in Section Barriers and Drivers of EcoSan Compost (e.g., Moya et al., 2019b; Sinharoy et al., 2019). Recommendations are based on the authors' expertise and are not exhaustive.

could extend the agricultural areas that could receive and benefit from ecological nutrient management using EcoSan compost. Long-term field trials across multiple soil types, crop types, and climates are needed to better quantify agronomic and ecological benefits and potential consequences of EcoSan compost use in agriculture.

We found distinct longevities of the carry-over effect of the soil amendments. The interannual boost in plant production after a one-time application of an organic matter amendment can be attributed to the slow-release of nutrients initially present in organic forms, as well as changes in soil properties that continue to promote plant production (Habteselassie et al., 2006; Ryals and Silver, 2013). We detected no carry-over effect for urea, indicating that the N that was not taken up by the crop within the first season is lost to the environment, rather than conserved in the soil (Peoples et al., 2004). In contrast, crop production was significantly greater than the control for two and four crop cycles for the biosolids and biofertilizer treatments, respectively. This result was surprising since biosolids contained more organic C and total N than the biofertilizer. A possible explanation is that there were greater N gaseous and leaching losses from the biosolids-amended soils, whereas unintended losses from the biofertilizer-amended soils were minimal. The carry-over effect lasting the longest was in the compost treatment. Crop production declined slightly in the second crop cycle, but was elevated by about two-times more than the control throughout all six crop cycles. The longer carry-over effect in the compost amended soils can be attributed, in part, to a greater amount of total N added in the compost treatment (6.46 gN/pot in Compost compared to 2.26 gN/pot for Biosolids and 0.61 gN/pot for Biofertilizer; **Table 1**) since treatments were applied based on equivalent PAN. However, differences in total N do not fully explain treatment differences in carry-over effect as evidenced by the longer carry-over effect of biofertilizer relative to biosolids. Compost may have also had a stronger improvement on soil structure and aggregate stability, which could have also contributed to the trends in water leaching.

Potential for Ecological Sanitation to Meet Sustainable Development Goal 2

Direct and indirect crop benefits from the application of organic matter amendments are widely documented across agricultural production systems (Diacono and Montemurro, 2011). By providing a source of essential macro- and micronutrients for plants, organic matter amendments can relieve nutrient limitations to productivity that are inherent in a soil or created by extraction through biomass harvesting or soil degradation. Nutrients that are complexed with organic matter become available through a microbially-mediated mineralization process, thus providing a slow-release fertilizer that benefits crop growth beyond a single growing season. Indirectly, organic amendments benefit crops by increasing the soil organic matter pool. Soil organic matter is associated with a multitude of biological, physical, and chemical soil functions and is a key component of soil health (Kibblewhite et al., 2008). This increase in soil organic matter stocks can foster more resilient and productive agroecosystems through improved soil health and soil structure. The nutrients and organic matter embodied in human excreta are a vastly underutilized resource to produce organic amendments. In our experiment, we found that EcoSan compost was an effective source of plant available nutrients. The organic matter embodied in the compost improved soil functions, which has been shown widely in land application studies that use compost from different feedstocks (e.g., Goswami et al., 2017; Bekchanov and Mirzabaev, 2018; Lehmann et al., 2020).

We considered the potential for nutrient recovery from human excreta to meet nutrient demand in Haiti. EcoSan is currently deployed at small- to medium-scales in Haiti, primarily through container-based sanitation coupled with centralized aerobic, thermophilic composting. Human feces, if collected and safely treated, could supply 13, 22, and 11% of the country's N, P, and K crop demand, as well as provide a source of organic matter. For perspective of the considerable potential for circular sanitation economies to supply nutrients for agriculture, human urine and feces has the potential to meet 22% of P demand on a global-scale (Mihelcic et al., 2011). Emerging technologies for nutrient recovery from urine, including alkaline dehydration (Simha et al., 2020), suggest higher potentials, with urine alone able to meet 35% of N and 25% of P demands (Simha, 2021). If nutrients were also recovered from urine in Haiti, an additional 83, 44, and 32% of the country's crop demand of N, P, and K could be met. In SOIL's current toilet design, urine is disposed of on-site due to difficulties with transporting large volumes of liquid. Therefore, future research and investment in urine nutrient recovery is needed to make significant advancements in achieving SDG 2 through circular sanitation.

Interactions With Other Sustainable Development Goals

Transitioning to ecological nutrient management using compost from closed-loop sanitation systems not only contributes to eliminating hunger (SDG 2), but also has reinforcing and indivisible interactions with multiple other SDGs, particularly the goals of clean water and sanitation for all (SDG 6) and climate change action (SDG 13; Nilsson et al., 2016). EcoSan technologies are designed with the explicit aim of returning nutrients to agricultural soil (Hu et al., 2016). In these closed-looped nutrient systems, the goals of providing safely managed sanitation and ending hunger worldwide are inextricably linked. We found that these goals are complementary. The sanitation process used in this study consumed little water compared to flush toilets (Haq and Cambridge, 2012), provided a safe and dignified sanitation option (Russel et al., 2015), and produced a nutrient-rich, pathogen-free compost (Berendes et al., 2015; Piceno et al., 2017). Compost yielded sustained increases in plant production for multiple crop cycles and was most adept at retaining water. These findings suggest that the land application of feces-derived compost increases the resiliency of agroecosystems.

Circular nutrient management through EcoSan can also be an important, and overlooked, climate change solution. EcoSan can support climate change solutions in five ways. First, greenhouse gas reductions can be achieved by converting from alternative waste management fates (Ryals et al., 2019; McNicol et al., 2020). Second, soil greenhouse gas emissions can be avoided from the displacement of mineral fertilizers by compost. In Haiti, mineral fertilizer use is very low (Bargout and Raizada, 2013), but this offset may be large in regions where fertilizers are commonly used. In our study, soil nitrous oxide emissions were least from composted soils and most from biosolids amended soils. Third, EcoSan can promote soil carbon sequestration. Compost has high potential to increase soil organic C pools in agricultural settings (Ryals et al., 2014; Paustian et al., 2016), but the extent to which compost derived from human feces impacts soil carbon has not been well documented. We found a significant increase in soil C from a one-time application of compost, an effect that was not observed in any other treatment. Fourth, increases in soil organic matter from EcoSan compost can help agroecosystems adapt to climate change by increasing resiliency to drought and flooding conditions. In this study, we also found that compost leached the least amount of water, suggesting increased soil water retention and greater water use by plants. Finally, EcoSan services themselves can be climate resilient in design by, for example, using container-based toilets that can be easily sealed with a watertight lid or elevated in the event of a flood.

Food insecurity (SDG 2) and poverty (SDG 1) are partially driven by low soil fertility, which is in turn influenced by farming and forestry practices. However, focusing on the roles of soil fertility and the farming decisions of smallholder farmers oversimplifies the drivers of these chronic problems and impedes our ability to meaningfully address the SDGs. In countries like Haiti, where colonial subjugation and later neoliberal economic subordination have shaped food systems, circular nutrient management may also offer an alternative natural resource that increases independence (Steckley and Shamsie, 2015; Trimmer et al., 2020). In addition to providing climate change solutions, EcoSan amplifies the positive effects of domestic food security and sanitation through increased domestic community self-sufficiency and reduced dependence on foreign food aid and agronomic intervention (Wanner, 2015). The establishment of a circular nutrient economy may offer an alternative to historical international efforts to reduce poverty by prioritizing a dependent, export-driven agro-economy (Otero et al., 2013). We show that the improvements to soil fertility and water retention in the closed-loop sanitation system are poised to increase crop production and potentiate economic growth at the local community scale without necessitating economically and ecologically unsustainable resource inputs (e.g., synthetic fertilizers, large scale irrigation). Current efforts by foreign countries and non-governmental organizations to "open" Haiti's food markets to be export-driven require an increase in synthetic fertilizer application from the low rate of nitrogenous fertilizer application of 7670 tons km-2 year-1 as of 2001 (Bargout and Raizada, 2013). The required inputs for increased export crop production would contradict the objectives of climate action (SDG 13) and making cities and human settlements inclusive, safe, resilient, and sustainable (SDG 11) by first increasing leaching and gaseous efflux of nutrients from soils, and then by making local communities vulnerable to foreign policies and the global economy, which have historically subordinated the Haitian (Otero et al., 2013). Finally, by increasing farmers' physical and financial access to locally derived nutrients for farming and therefore their potential income, implementation of EcoSan systems may serve to promote economic equality within strongly class-stratified societies like Haiti.

Barriers and Drivers of EcoSan Compost

Current ecological, institutional, and cultural barriers hinder the widespread implementation of coupled sanitation-agriculture systems (**Table 4**). EcoSan toilet user attitudes toward source separation and nutrient recovery may be agreeable (Lamichhane and Babcock, 2013; Russel et al., 2015; Simha, 2021), yet other barriers likely impede the large-scale adoption of these practices. For example, a recent multinational survey by Simha (2021) demonstrates that among university community members, there was greater acceptance for human urine recycling than acceptance of disposal, and widespread belief that human urine can be safely used as a crop fertilizer. However, of all options to manage human urine, sending it to a wastewater treatment plant (WWTP) was the most popular among respondents. They argue that for widespread acceptance, urine-diverting sanitation systems must be connected to treatment systems that function as well as or better than WWTPs. 17 Simha et al. (2017) identified and analyzed factors affecting farmers' attitudes on human waste recycling in Vellore district, India. A lower willingness to recycle feces they attribute in part to "faecophobia" and assert that while there may be cultural underpinnings to this view, more work should be done to understand the origins of faecophobia rather than assume that feces recycling should not be pursued due to persistent disapproval. Recent work by Fischer et al. (2021) emphasizes the need for recognition of the social and political context in which a sanitation technology is situated, in reference to the business failure of the Peepoo toilet bag in Nairobi, Kenya.

In the specific context of SOIL, a 2015 study following SOIL's service pilot found that 71% of participating households were willing to pay to continue receiving the container-based EcoSan service (Russel et al., 2015). However, in 2019, Russel et al., identified challenges related to large-scale implementation container-based sanitation EcoSan, including the higher operational cost due to providers addressing the full sanitation value chain. However, they suggest that container-based sanitation may ultimately be more cost-effective by using novel treatment technologies that include resource recovery. Here, we provide a summary of barriers to widespread implementation of EcoSan systems and recommendations to overcome barriers based on literature and practical experience (**Table 4**), with a specific focus on ecological barriers. Our research provides new data on the agronomic and ecological drivers of EcoSan compost.

Ecological barriers to widespread adoption of EcoSan compost can be addressed through knowledge sharing, assessment of local resources, and new scientific research. Chemical fertilizers are often promoted through agricultural extension and subsidized by government programs (Moya et al., 2019b). Education about the importance of soil health promoting practices such as organic amendment application, and studies on the long-term effects of feces-derived compost could shift culture away from exclusive reliance on chemical fertilizers. Composting requires addition of a C-rich bulking agent (e.g., sugarcane bagasse) to maintain an optimal C:N ratio for aerobic decomposition (Moya et al., 2019b). Adequate bulking agent must be supplied and maintained at the user level for application after toilet use and be available to the composting facility for large scale thermophilic composting (Russel et al., 2019). Regional agroecological and economic analyses could supply valuable data on the availability and feasibility of various organic waste streams to serve as compost bulking agents.

Limitations and Future Research Directions

We found that soil amendments derived from human excreta promoted plant production and improved soil nutrient cycling compared to urea, a nitrogen-based fertilizer, in a greenhouse study. Further, we found significant carry-over effects for potted soils amended with EcoSan compost. While these results point to the promising role of human excreta in contributing to the SDG 2 goal, there are some limitations to our study that require further research. The fertilizer comparison used in this study was urea, a N-based fertilizer that did not contain other macro- or micronutrients that can also limit plant growth. We were unable to quantify gaseous fluxes of ammonia, which is often the major N loss pathway from urea fertilization of soil (Rawluk et al., 2001). Our results are also constrained by methodological limitations of pot studies, including controlled environmental conditions that are different from field conditions and disturbance of soil physical and biological properties (Dalling et al., 2013).

Multiple knowledge gaps on the ecological benefits and risk of composted human feces must be addressed to fully realize the potential of EcoSan as a solution to hunger. Detailed land application studies on the effect of various application rates of composted feces on crop yield, greenhouse gas emissions, soil carbon sequestration, and soil health could supply site-specific data. This would enhance the capacity of local agricultural extension and technical assistance agencies to promote composted feces. Studies should include the net climate change mitigation potential of compost application to proximate cropland, accounting for transport costs of bulky compost material. Evaluations of the sustainability of EcoSan must also include risk assessments of potential inadvertent consequences to human health. Risks of the fate and transport of pharmaceuticals, persistent pollutants, and other emerging contaminants in EcoSan products should be better understood in order to develop strategies to minimize risks to people and the environment (Krause et al., 2021).

CONCLUSION

The capture of human excreta and its transformation into a resource for agricultural is an underutilized solution toward ending hunger. We show that soil amendments derived from human waste had multiple benefits to crop production and soil nutrient cycling. EcoSan compost boosted plant production, which remained elevated relative to control after six consecutive crop cycles. This finding indicates there are both short-term benefits from plant-available nutrients and long-term benefits to soil health and nutrient mineralization. Transformation of human feces and recycling as a soil amendment could potentially provide 13, 22, and 11% of annual crop N, P, and K demand within Haiti, a country with an urgent need for both improved sanitation and soil restoration. Urine, which is currently not included in local EcoSan nutrient recovery systems, could provide an additional 83, 44, 32% of annual crop N, P, and K demand in Haiti. Thus, EcoSan compost can contribute to SDG 2 by creating resilient and productive agroecosystems, particularly those farmed by small-scale producers, and also intersects with multiple sustainable development goals.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

RR and KP contributed to conception and design of the study and performed the statistical analysis. RR and SH collected and analyzed soil, plant, water, and gas samples. RR wrote the first draft of the manuscript. EB and SP wrote sections of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.716140/full#supplementary-material

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REVIEW
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Restoring Soil Fertility on Degraded Lands to Meet Food, Fuel, and Climate Security Needs via Perennialization

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A continuously growing pressure to increase food, fiber, and fuel production to meet worldwide demand and achieve zero hunger has put severe pressure on soil resources. Abandoned, degraded, and marginal lands with significant agricultural constraints—many still used for agricultural production—result from inappropriately intensive management, insufficient attention to soil conservation, and climate change. Continued use for agricultural production will often require ever more external inputs such as fertilizers and herbicides, further exacerbating soil degradation and impeding nutrient recycling and retention. Growing evidence suggests that degraded lands have a large potential for restoration, perhaps most effectively via perennial cropping systems that can simultaneously provide additional ecosystem services. Here we synthesize the advantages of and potentials for using perennial vegetation to restore soil fertility on degraded croplands, by summarizing the principal mechanisms underpinning soil carbon stabilization and nitrogen and phosphorus availability and retention. We illustrate restoration potentials with example systems that deliver climate mitigation (cellulosic bioenergy), animal production (intensive rotational grazing), and biodiversity conservation (natural ecological succession). Perennialization has substantial promise for restoring fertility to degraded croplands, helping to meet future food security needs.

Keywords: degraded lands, marginal lands, soil fertility, soil carbon, soil nitrogen, soil phosphorus, bioenergy, rotational grazing

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INTRODUCTION

The continuously growing pressure on agricultural lands to increase food production has severely tested their capacity to produce agricultural products at an acceptable environmental cost. Estimates suggest that if current trajectories continue, 840 million people will be affected by hunger by 2030 (FAO et al., 2021). And some contend that by 2050 food production will need to double or more to meet the demands of a growing global population that is ever more affluent (Food Security Information Network, 2017). However, many lands that are already in use or have previously been used for food production are agronomically degraded. Decreased soil fertility and increased environmental sensitivity to farming due to poor soils or poor management or both have steadily reduced yields on these lands. Many once arable lands are now unsuitable for agriculture, and many have been abandoned from agriculture.

Degraded lands often result from reduced soil fertility stemming from intensive management, poor soil conservation measures, and climate change. Innumerable studies have documented the negative impacts of intensive annual crop production on the soil environment—indeed, the current resurgence of interest in regenerative agriculture (sensu Francis et al., 1986; Giller et al., 2021) has the restoration of soil health as a central tenet (Schreefel et al., 2020). Some specific aspects of intensive annual crop production that lead to soil degradation include frequent disturbance events such as tillage, the absence of continuous year-round plant cover, the lack of continuous deep rooting systems and crop functional diversity, and unbalanced nutrient budgets. Additionally, climate change—increased warming and changing precipitation dynamics worldwide—has accelerated or exacerbated soil degradation in regions where soils are increasingly subjected to flooding and drought (Intergovernmental Panel on Climate Change, 2019). Erosion losses have been particularly severe—up to 1% of topsoil is lost yearly in many places (Montgomery, 2007), the result of tillage, overgrazing, and the growing incidence of extreme climate events that accelerate both wind and water erosion.

The continued use of degraded lands for agricultural production requires ever-increasing management interventions to enable high-yielding food production. In this context, further land degradation represents an additional threat to agriculture's environmental integrity by exacerbating soil carbon (C), nitrogen (N), and phosphorus (P) losses. The loss of C and essential nutrients from the agricultural system results in land that struggles to produce nutritious food for human consumption (FAO, 2019), and losses will only increase as management intensifies to replace lost fertility, creating a positive, downward spiraling feedback loop.

Estimates of the extent of degraded lands worldwide differ markedly depending on the definition. Defined most commonly as lands with reduced productivity due to human activity (Oldeman et al., 1990) leaves wide latitude to estimates of its extent, which range globally from 0.5 to more than 6 billion ha (Gibbs and Salmon, 2015). Narrowing the definition to perhaps its most severe agricultural extent—former agricultural land now abandoned—yields a more restricted estimate of 864 to 951 million ha (Campbell et al., 2008), though still highly uncertain (Gibbs and Salmon, 2015). In the United States alone, estimates based on county land-use records (Campbell et al., 2013) and satellite observations (Cai et al., 2011) suggest a range of 74–99 million ha. We focus here on this narrower definition of degraded lands—croplands or pastures that might, with proper management, be restored and made productive again without long-term consequences to environmental health. Such management might include biologically based practices that promote soil health and recouple C, N, and P cycles through a systems-based approach, focused on improving nutrient retention and balancing nutrient budgets, rather than, for example, fertilizer additions intended to maintain high inorganic nutrient levels in soils (Drinkwater and Snapp, 2007; International Fertilizer Industry Association, 2009). Ecological nutrient management (Drinkwater et al., 2008) is intrinsic to organic, sustainable, and regenerative agriculture (Edwards et al., 1983; Robertson and Harwood, 2001; Giller et al., 2021) and is achieved principally by improving plant diversity, including the incorporation of perennials into long rotations.

We also consider restoring fertility for a newly recognized class of contemporary cropland—subfield areas with consistently low and unprofitable yields. Satellite-based yield stability analyses suggest that >20% of maize (*Zea mays* L.) and soybean (*Glycine max* L. Merr) fields in the US Midwest may fit this classification (Basso et al., 2019). Moreover, precision farming technologies (such as identifying under-performing subfield areas and converting them to perennials) create additional potential for restoring the productive capacity of these lands with perennial cropping strategies (Brandes et al., 2018). Subfield variability of this sort likely occurs worldwide.

The restoration of degraded soil fertility via natural perennialization is a longstanding farming practice in place for millennia. Shifting cultivation, known by different names in different regions of the world, and in widespread use worldwide until the Eighteenth century and in the pantropics into the Twentieth century, has as a central tenet the restoration of soil fertility during a natural fallow phase after intensive cropping (Nye and Greenland, 1960; Irvine, 1989; Robertson and Harwood, 2001; Sandor et al., 2007; Schmidt et al., 2021). The natural fallow provides an unmanaged period during which ecological succession restores soil fertility to a point where soil can again be "mined" for agriculture.

That ecological succession restores soil fertility—or, in the case of primary succession, creates soil fertility—is a longstanding ecological principle (Odum, 1969). In primary succession newly exposed parent material is successively colonized by lichens, grasses, forbs, shrubs, and eventually trees, together with a more and more complex soil ecological community that develops as soil organic matter accumulates and N, P, and other nutrients cycle quickly enough to support accelerating primary productivity (Gorham et al., 1979). Secondary succession follows a disturbance that resets the successional clock to some earlier time but does not remove soil and depending on the disturbance—be it fire, extreme weather, agriculture, or some other perturbation—a similar but faster sequence of recovery takes place, eventually, in the absence of continued disturbance, restoring the system to some pre-disturbance state. In one sense, annual cropping systems are caught in an early successional cycle, whereby the ecological clock is reset annually with crop harvest (Robertson and Paul, 1998; Crews et al., 2016). Essential nutrients are readily lost from early successional systems and tightly conserved later, when perennial biomass is rapidly accumulating (Vitousek and Reiners, 1975), which helps to explain the contribution of perennial vegetation to nutrient retention and system-wide nutrient use efficiency. Incorporating perennials into cropping systems to restore fertility and retain nutrients thus draws on ecological theory and a long history of worldwide practice.

Growing evidence suggests that degraded lands also have the potential for restoration while remaining productive (Asbjornsen et al., 2013; Bell et al., 2020). In almost all cases, perennialization—the incorporation of perennial crops and forages in long rotations—is key. Perennialization can be applied in many different systems to enhance the delivery of ecosystem services from agriculture (e.g., Syswerda and Robertson, 2014; Snapp et al., 2015; Schulte et al., 2017), including fertility restoration (Asbjornsen et al., 2013), soil C accretion (Bell et al., 2020; Ledo et al., 2020), N availability (Burke et al., 1995; Reeder et al., 1998; Tufekcioglu et al., 2003), and P retention (Patty et al., 1997; Crews and Brookes, 2014), all important components of ecological nutrient management.

Here we synthesize the advantages of and potentials for using perennial crops to restore soil fertility on degraded lands and their ecosystem functions (**Figure 1**). In particular, we identify the mechanisms whereby perennial crops enhance and restore C, N, and P cycling using a systems approach. Further, we illustrate alternative management strategies, barriers to adoption, and potential solutions to restore degraded lands via cropping system management might help to meet future food security needs (FAO, 2019).

IMPACTS OF PERENNIALIZATION ON FERTILITY RESTORATION

The central attributes of ecological nutrient management are more efficient nutrient cycling and greater retention of C, N, and P, which are particularly important for sustaining yields in agriculture. Soil C, N, and P stores are key indicators of soil health, and almost always associated with other aspects of soil quality—physical characteristics (including improved infiltration, soil structure, porosity, and aggregate stability), chemical characteristics (including nutrient availability and retention), and biological attributes (including soil food web complexity and pest and pathogen suppression).

Soil Carbon Accrual

There is perhaps no better metric to characterize soil fertility than soil organic matter or soil organic C (SOC) levels. Any activity that leads to SOC accrual benefits the system with increases in soil water holding capacity, nutrient storage and retention (N and P, among others), cation exchange capacity, soil porosity, erosion resistance, soil biota habitat, and any biologically mediated process dependent on C. Soil fertility restoration thus relies heavily on SOC accrual, with strategies to promote C accretion depending on crop type, agricultural management, and organic amendments.

Conventional agricultural practices tend to promote SOC loss. In particular, tillage stimulates the oxidation of soil organic matter, simplifies microbial populations (especially fungal; Helgason et al., 2010), and accelerates erosion, all leading to lower SOC pools, poor soil fertility, and land degradation. Additionally, annual crops contribute relatively little C belowground. In a typical annual cropping system, only a small proportion of total plant biomass is comprised of roots, ready to contribute to stable SOC through turnover and exudation. Root-to-shoot ratios of annual crops are typically <0.30 (**Table 1**) or <25% of total plant biomass. This is significant for SOC accretion because root derived-C appears to contribute more to SOC stabilization than does aboveground residue, whether the SOC is mineral-associated C (e.g., Kong and Six, 2010; Austin et al., 2017; King et al., 2020) or particulate organic C (e.g., Puget and Drinkwater, 2001; Cates et al., 2016).

Conversely, perennial cropping systems tend to promote SOC accretion, which results from several attributes (Anderson-Teixeira et al., 2009; Agostini et al., 2015). First, the root-to-shoot ratios of perennial crops are high, typically much >1 and 3–20 times those of maize (**Table 1**; Ma et al., 2001; Frank et al., 2004; Bonifas et al., 2005; Dietzel et al., 2017). Perennial plants also tend to have longer growing seasons which contributes to more root biomass production (Dohleman and Long, 2009; Ferchaud et al., 2016). Relatively large and deep rooted systems correspond with greater root-associated C inputs (Rasse et al., 2005; Anderson-Teixeira et al., 2009; Agostini et al., 2015). In one synthesis, Anderson-Teixeira et al. (2013) found that a shift from annual conventional systems (e.g., maize-soybean rotations) to perennial crops increased belowground C allocation by >400%, associated with increases in root biomass of up to 2,500%.

Greater root biomass also implies greater rates of root exudation, known to increase and improve soil aggregation, which protects soil C from microbial attack. Thus, one can expect that more roots throughout the soil profile will increase aggregation at many different soil depths (Liebig et al., 2005; Kutsch et al., 2009; Stockmann et al., 2013; Cates et al., 2016). Aggregation not only protects soil C, assuring longer C residence times but also has positive implications for soil water holding capacity and water infiltration (Bharati et al., 2002; Hernandez-Santana et al., 2013; Huang et al., 2014; McGowan et al., 2019). Soils with high levels of aggregation are better able to withstand large precipitation events because water can more quickly infiltrate into deeper depths than soils with poor structure. Improved water infiltration thus reduces runoff of plant available water and essential nutrients, improving water availability over time and helping these systems to be more resilient to extreme weather events (Steward et al., 2011).

The absence of soil disturbance further contributes to SOC gains—in continuous perennial systems, tillage is used only in establishment years, such that afterwards permanent plant cover and better soil structure leads to reduced erosion, lowered decomposition rates, and greater aggregate stability. The use of perennial crops also has the potential to increase the amount, and the diversity of organic inputs returned to the soil when included in any given system. Longer growing periods and less biomass removals during harvest from perennial crops result in more ground cover and more biomass to be returned to the soil, resulting in more SOC.

Diversity *per se* can also boost SOC accrual, in perennial as in annual systems, leading to more diverse soil microbial communities (Tiemann et al., 2015; Sprunger et al., 2020) and more microbial biomass C (Spehn et al., 2000; Zak et al., 2003). More microbial diversity and biomass C can also enhance soil pore formation (Kravchenko et al., 2019) and aggregate stability facilitated by fungal hyphae and microbial extracellular compounds (Helgason et al., 2010; Tiemann et al., 2015). Further, microbial biomass and decomposition byproducts can stimulate gains in mineral-associated organic matter fractions (Carrington

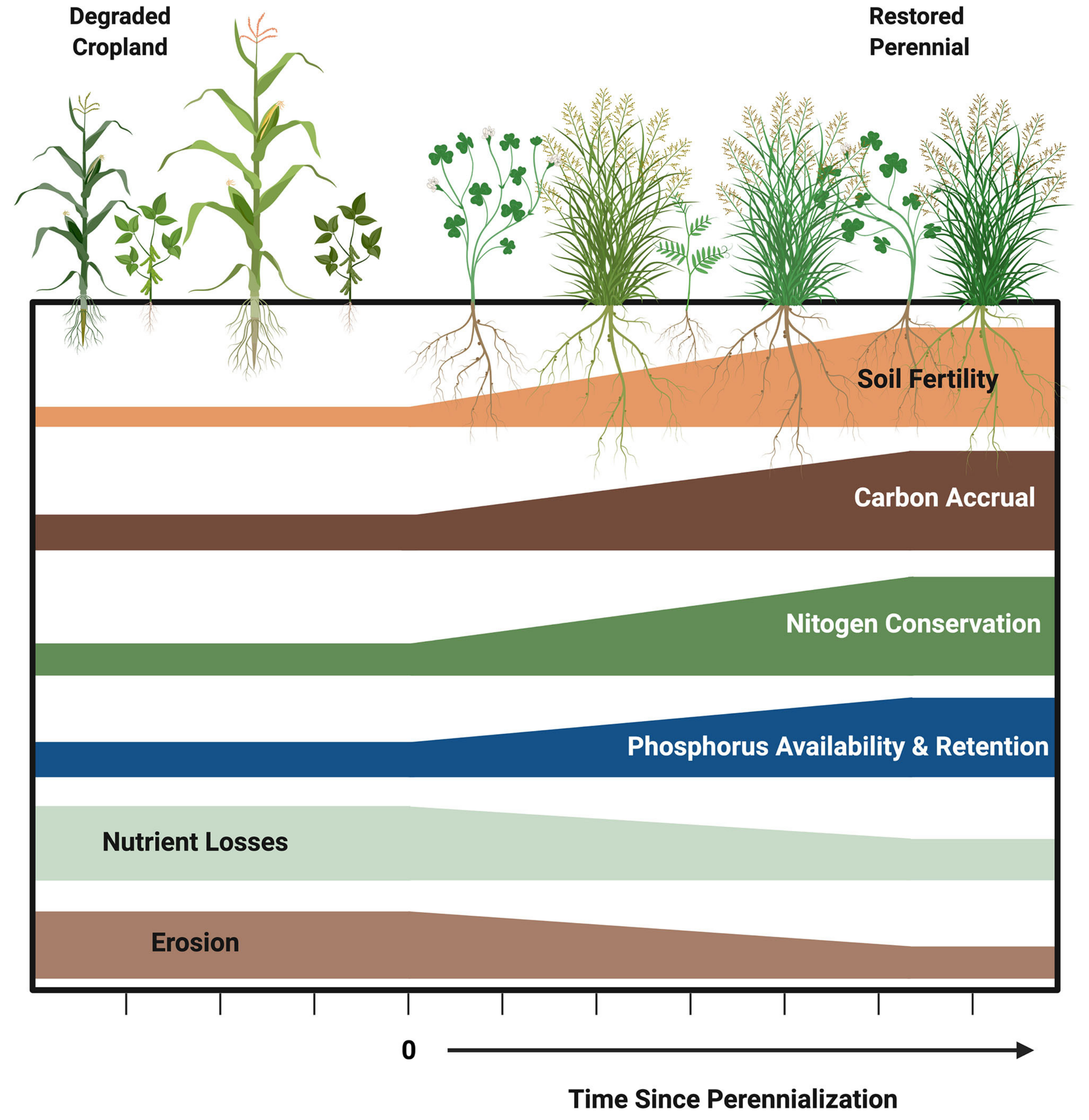

FIGURE 1 | Patterns of key agronomic and biogeochemical process changes during the restoration of soil fertility via perennialization of degraded cropland.

et al., 2012; Miltner et al., 2012) and thus stable C stores. Diversity can also promote soil C accrual through interspecific root C transfer, whereby systems with species that participate in such transfers gain stable C at faster rates (Kravchenko et al., 2021). In addition to impacts on SOC accrual, plant diversity can also enhance pest (herbivore, weed, and disease) suppression, pollination, and other ecosystem services (Gallandt et al., 1999; Abawi and Widmer, 2000; Robertson et al., 2014; Landis, 2017).

Nitrogen Conservation

Nitrogen is one of the most important and dynamic elements that limit terrestrial plant growth (Lebauer and Treseder, 2008). Though N fertilizer is commonly added to agricultural ecosystems, it is energy-intensive and expensive to produce and typically results in large N losses that harm the environment and human health (Robertson and Vitousek, 2009): Less than half of the N fertilizer applied to agricultural lands globally is

TABLE 1 | Root-to-shoot ratios of annual and perennial crops measured at the end of the growing season.

Crop	Root-to-Shoot ratio	References
Annual crops		
Maize	0.09	Ordóñez et al., 2020
Maize	0.17	Allmaras et al., 1975
Soybean	0.21	Ordóñez et al., 2020
Soybean	0.14	Allmaras et al., 1975
Spring wheat	0.33	Sainju et al., 2017
Perennial crops*		
Switchgrass	1.39	Sainju et al., 2017
Switchgrass	6.11	Ma et al., 2001
Intermediate wheatgrass	1.89	Sainju et al., 2017
Smooth bromegrass	2.51	Sainju et al., 2017

All perennial stand ages are between 4 and 6 years.

recovered at harvest (Lassaletta et al., 2014); the rest is lost to the environment, where it promotes the eutrophication of surface waters, causes marine dead zones, pollutes groundwater drinking supplies, suppresses biodiversity, and contributes to global warming, ultimately threatening long-term food security.

Soil N stocks tend to be severely depleted in degraded lands, making production on these lands even more dependent on external N sources. At the same time, production becomes less responsive to N inputs owing to other constraints on soil fertility, such as low soil organic matter (section Introduction). The net result is even lower N use efficiency, making these systems ever more leaky and environmentally harmful and exacerbating soil degradation in an unfortunate downward spiral.

Nitrogen conservation is thus a cornerstone of regenerative agriculture (Robertson and Harwood, 2001) and sustainable intensification (Pretty, 2018; Spiegal et al., 2018), is central to ecological nutrient management and can be readily evaluated by considering the balance of N inputs and outputs. Cropping systems with high N use efficiency—where N outputs other than harvest are low relative to inputs—will conserve N. Or, put another way, in N-conserving systems, most N inputs will become part of the harvest or be stored in soil organic matter, ready to supply N to a succeeding crop. This can be seen in side-by-side comparisons of fertilized perennial vs. annual cropping systems, where N use efficiency (the amount of N removed relative to fertilizer inputs) is substantially higher for perennial systems (**Table 2**). Perennial crops—whether harvested, grazed, or used for conservation plantings—have a naturally high potential for conserving N for a variety of reasons and additionally can have novel N acquisition strategies that can minimize their needs for fertilizer N.

Perennial crops are highly N use efficient due to a combination of harvest stoichiometry, translocation abilities, long growing seasons, and extensive root systems. First, with the exception of forage legumes and seed crops, relatively little N is removed in perennial harvests. This is because the N content of non-reproductive biomass is commonly several times lower than that of seeds and grain, with their high protein contents and low C:N ratios. This is especially true when harvest occurs post-senescence, when the N content of biomass can be well-under 1% due to N translocation to roots. In grazed systems, "harvests" occur in-season as forage is consumed, but most of the N in this biomass is immediately returned to the pasture as urine and manure. However, this is not as true for forage crops harvested during the growing season for later consumption, when substantially more N can be removed, especially by legumes such as alfalfa (*Medicago sativa*) that have especially high biomass N contents.

Low post-senescence N contents reflect the ability of perennial plants to translocate N from aboveground leaves and stems to belowground roots, rhizomes, and root crowns prior to senescence (Vergutz et al., 2012). The N stored will then be re-translocated aboveground for use during the next growing season (Yang and Udvardi, 2018), reducing the need for new N. Nitrogen resorption efficiencies for perennial grasses can be >75% (Vergutz et al., 2012) but can also vary substantially even within cultivars of the same species (Yang et al., 2009; Roley et al., 2020), as well as with stand age (Propheter and Staggenborg, 2010). Although N fertilization can increase resorption efficiency—more N gets translocated belowground even when there is no productivity response—it also can lead to higher post-senescence leaf N content, leading to less N conservation overall (Jach-Smith and Jackson, 2015).

Longer growing seasons for perennials also contribute to N conservation. Synchrony between N mineralized from soil organic matter, and plant N uptake is an important N conservation mechanism in most terrestrial ecosystems (Robertson, 1997). In perennial systems, plant growth typically starts earlier in the spring and persists longer into the fall, leading to a greater proportion of the growing season with active N uptake as compared to most annual crops (Culman et al., 2013). Since microbes are active throughout this period and more, in perennial systems, more of the N they mineralize will be immobilized by plants, leaving less to be lost to the environment (Sprunger et al., 2018).

Finally, as noted earlier, perennial plants tend to have deeper and more extensive rooting systems—about 3 to 8 times more extensive than annual crops (Anderson-Teixeira et al., 2013; Dietzel et al., 2017), with root:shoot ratios of 2 to 3 times higher than for annual crops (**Table 1**). This provides an enhanced potential to capture inorganic N, whether naturally mineralized from soil organic matter or added in fertilizer, before it leaches from the soil profile. Lower leaching rates for both nitrate (Syswerda et al., 2012; Smith et al., 2013; Hussain et al., 2019) and dissolved organic N (Hussain et al., 2020) have been documented in a variety of herbaceous crops and short-rotation trees relative to adjacent annual crops, as well as in conservation strips (Schulte et al., 2017).

All cropping systems must acquire N to replace that removed in harvest or lost to the environment via leaching, volatilization, or denitrification. Perennial cropping systems are no different than annual in this respect, although their losses to the environment are typically lower, as noted above. Nonetheless, to maintain productivity, lost N must be replaced through biological N fixation (BNF), atmospheric deposition, or fertilization. In

TABLE 2 | Crop yields, nitrogen removal, and nitrogen use efficiency (proportion of fertilizer removed at harvest) in alternative annual and perennial cropping systems at the Bioenergy Cropping Systems Experiment at the W. K. Kellogg Biological Station, Hickory Corners, Michigan in 2014.

Cropping system	Crop	Harvest biomass Mg ha^{-1}	*N* removal kg N ha^{-1} yr^{-1}	*N* use Efficiency %
Annual cropping systems				
Continuous maize	Grain	11.4 ± 0.3	68.0 ± 3.6	40.7
Continuous maize + cover crops	Grain	9.7 ± 0.4	57.7 ± 3.0	34.6
Maize-Soybean rotation + cover crops	Grain	9.8 ± 0.4	62.1 ± 3.4	37.2
Perennial cropping systems				
Monoculture switchgrass	Biomass	8.5 ± 0.4	50.0 ± 3.3	89.3
Monoculture miscanthus	Biomass	21.9 ± 0.3	87.4 ± 4.9	>100.0
Polyculture native grasses	Biomass	6.5 ± 0.9	34.5 ± 4.3	61.6

**All perennial stand ages are 6 years old. Maize received 167 kg N ha^{-1} yr^{-1} of N fertilizer and perennial crops 56 kg N ha^{-1} yr^{-1}.*
Data are means (n = 5) ± standard error. Unpublished data.

non-harvested systems such as conservation plantings, losses can be extremely low in the absence of fire, and atmospheric deposition inputs on the order of a few kg per ha per year may be sufficient to meet most long-term N needs. But for harvested systems or unmanaged systems periodically burned, BNF or fertilization must make up for lost biomass N and must additionally be sufficient to provision accumulating soil organic matter, which might be 5% N at typical arable soil C:N ratios of 10:1. So degraded land regenerating soil fertility at a typical C accretion rate of 0.2 Mg C ha^{-1} yr^{-1} would sequester ∼20 kg N ha^{-1} yr^{-1}.

Long-term unfertilized perennial grasslands harvested for hay for >50 years (Jenkinson et al., 2004) show no declines in soil C and N stocks or yields, suggesting that N stasis is maintained largely through BNF. Likewise, that perennial herbaceous crops harvested for bioenergy are often unresponsive to N fertilizer suggests significant BNF inputs. At a site in the upper Midwest U.S., for example, Roley et al. (2018) found no response of switchgrass to N fertilizer in most years, and for a three-year period following two establishment years calculated an average minimum annual N deficit of 58 kg N ha^{-1} based on N mass balance. Biological N fixation—presumably associative N fixation—must have been at least this high to balance known losses from yield plus losses from leaching and denitrification and immobilization of N in soil organic matter, based on N mass balance.

Symbiotic BNF is well-known in legumes; agriculturally important perennials known to host rhizobia capable of N fixation include the herbaceous crops alfalfa and medic (*Medicago* spp.), clover (*Trifolium* spp.), vetch (*Vicia* spp.), and birdsfoot trefoil (*Lotus corniculatus*), as well as woody species like *Leucaena*, *Gliricidia*, and locust (*Robinia* spp.). In degraded soils, legumes can meet up to 90% of their N needs with atmospheric N_2 (i.e., via BNF), and the inclusion of legumes in pastures is a well-known strategy for intensifying forage production.

Less is known about associative N fixation (Smercina et al., 2019; Roley, 2021), which appears as a casual and episodic association between plants and free-living diazotrophic bacteria. Associative N fixation appears to occur most commonly on or adjacent to root surfaces or, at least in sugarcane (*Saccharum officinarum* spp.), also within plant stems, where the bacteria have ready access to labile C. Nitrogenase, the enzyme complex responsible for transforming atmospheric N_2 to a form that plants can use, is exquisitely sensitive to oxygen (Robertson and Groffman, 2021), making BNF difficult outside of the specialized nodules created by legumes and actinorhizal plants to exclude oxygen. Consequently, associative N fixation is slow, spatially discrete, perhaps episodic (Roley et al., 2019), and in any case hard to measure directly. Field measurements have detected major crops such as sugarcane and grasses that benefit from this type of association with N fixers (Boddey and Dobereiner, 1995; Peoples et al., 2001; Roley et al., 2018, 2019). Nevertheless, associative N fixation is being increasingly documented in a wide variety of ecosystems (Reed et al., 2011; Ladha et al., 2016) and attracting renewed attention as a low-cost source of N for perennial bioenergy crops. Although in some cases fertilizer N may still be needed to optimize production, including legumes in bioenergy species mixes would be an additional way to keep system-wide N use efficiency high. Annual crops that rely exclusively on BNF are known to have a higher system-wide N use efficiency (Córdova et al., 2019), and the potential for BNF's improving the N use efficiency of degraded lands through perennialization is equally promising.

Phosphorus Availability and Retention

Behind N, P is the second most limiting nutrient for plant growth. As an essential nutrient, P is crucial for the structure of DNA and RNA, enzyme production, and for ATP. Thus, P can co-limit plant productivity alongside N or even directly limit productivity in highly weathered soils where P supply is low (Elser et al., 2007). Unlike N, global stores of fertilizer P are limited and must be mined rather than synthesized from an unlimited atmospheric source. In addition to being in limited supply, around 50% of P losses are attributed to erosion, making P a strong environmental pollutant that contributes to poor water quality downstream (Alewell et al., 2020). Despite its importance, P cycling from a biological standpoint is under-studied, in part because P is more difficult to trace than C and N (Guignard et al., 2017). Yet, in degraded lands, P availability can be as severely compromised as C stores and N availability (Schneider et al., 2019).

Soil P is present in organic and inorganic forms, but only inorganic P is available for plant uptake. And like N, not all soil inorganic P is directly available to plants. Inorganic P is present in most soils as minerals such as apatite (a form of calcium phosphate), which must be weathered to an inorganic form available to plants. Additionally, P can be adsorbed to mineral surfaces such as clays containing iron and aluminum. This adsorbed P must undergo desorption reactions to become a soluble form available for plant uptake. Alternatively, organic P in plant residues, microbial biomass, and animal residues such as feces and urine can be mineralized to $HPO_4{}^{-2}$ for uptake. The organic P pool is dynamic and one of the most important sources of P availability in arable soils (Alewell et al., 2020), especially in organic, low-input, regenerative, and other systems that rely principally on biological nutrient sources.

Many degraded agricultural lands have abundant soil P but not in a form available to plants (Al-Abbas and Barber, 1964). Therefore, the processes that release plant-available P are important for sustainable P cycling. Factors that contribute to low plant-available P include fewer root exudates and microbial products that can aid the dissolution of P into plant-available forms (Graustein et al., 1977; Fox et al., 1990; Ingle and Padole, 2017), low pH, which can contribute to P adsorption by iron and aluminum, and high pH, which can contribute to P adsorption by calcium. Additionally, low levels of soil organic matter can reduce the amount of P available for dissolution insofar as soil organic matter also provides binding sites for soil inorganic P (Deb and Datta, 1967; Hue, 1991). Because the processes involved in P availability and retention have been largely ignored, degraded lands rely heavily on the addition of inorganic P fertilizers to meet plant demand and maintain plant productivity. However, much of the added P will not be returned to the soil as it will be harvested in plant biomass or lost to the system through erosion, runoff, and leaching (Bennett et al., 2001; Childers et al., 2011), further exacerbating the lack of available P in degraded systems.

Perennialization can improve P availability and recycling by reducing P losses and increasing the presence of plant-available P (Patty et al., 1997; Lehmann et al., 2001; Crews and Brookes, 2014). There are many different mechanisms by which this occurs. As previously noted, perennial crops increase soil organic matter, which can enhance P cycling by providing a source of P via decomposition or dissolution of adsorbed inorganic P (Kang et al., 2009; Gaxiola et al., 2011). Phosphatase enzymes produced by soil microbes can selectively cleave P esters from organic matter, allowing P to be immobilized in microbial biomass (van der Heijden et al., 2008; Richardson et al., 2009), which can lead to more P recycling when microbes die. The processes involved with the release of plant-available P are facilitated in perennial cropping systems through enhanced root biomass and rooting depths and through enhanced microbial biomass and activity.

Deeper and more diverse rooting systems, as well as enhanced microbial communities, can also contribute to more efficient P availability and recycling (Crews and Brookes, 2014). The release of P from minerals and organic matter can occur through root exudation of organic acids and through microbial activity. Organic acids produced by roots and microbes break down soil minerals and compete for organic matter adsorption sites to release plant-available P (Deb and Datta, 1967; Fox et al., 1990; Hue, 1991). There is a positive correlation between the amount of organic acids in soil and plant productivity due to P availability (Bolan et al., 1994). More roots at deeper soil depths increase the amount of root exudates and ultimately the amount of P available for plant growth. Microbes are also crucial for transforming P into plant-usable forms by exuding metabolites and organic acids that release adsorbed, unavailable P from minerals and organic matter (Graustein et al., 1977; Ingle and Padole, 2017). Mycorrhizae that are associated with plant roots are particularly important at facilitating this process (Malajczuk and Cromack, 1982; Lapeyrie, 1988), making P more available and enhancing plant uptake of P. Therefore, having an active, diverse microbial community will facilitate P dissolution and mobilization and ultimately the availability in soils.

Not only do perennial systems provide more plant-available P through an increase in root and microbial processes, but they also lead to P retention in the system. When P is not associated with minerals, organic matter, or biomass, it can easily be lost from the system through runoff and erosion (Bennett et al., 2001; Childers et al., 2011). For example, across the globe, agricultural crop fields lose ∼15 million tons of P due to erosion (Smil, 2000). And Cordell et al. (2009) estimated that globally, 8 million Mg of P are lost from agricultural fields every year largely due to an imbalance of P fertilizer application rates and plant uptake rates, resulting in the overapplication of P in cropping systems. Patty et al. (1997) found that even small perennial grass buffer stirps were enough to reduce P runoff into water bodies by 89–100%, though it would be better if the P remained in the fields available for future uptake. Root and mycorrhizae uptake of P also helps ensure that the P is not lost from the system. The greater abundance of roots and mycorrhizae in perennial systems increases the probability that P uptake will occur, as root length, root surface area, and mycorrhizae strongly correlate with P uptake (Bolan, 1991; Pang et al., 2010). While P exports from harvested perennial biomass such as alfalfa can be large, less P is removed from the system compared to annual plants such as corn and soybean (Lehmann et al., 2001; Cadot et al., 2018; Cooney, 2019). Perennialization of degraded lands will keep more plant residues and canopy cover in place for longer periods of time. Thus, these lands will be less likely to lose P through erosion, leaching, or runoff.

POTENTIAL MANAGEMENT STRATEGIES FOR RESTORATION

To illustrate the mechanisms underpinning perennialization's impact on soil fertility restoration we describe below three potential management systems that differ in intensity, impact, and time to full restoration, broadly illustrating three overarching uses—climate change mitigation (bioenergy cropping systems), animal protein production (intensive rotational grazing), and biodiversity restoration (conservation plantings). All three provide complementary mixes of ecosystem services as diagrammed in **Figure 2**, and none are exclusive—these and other regenerative systems could be established in the same landscape—indeed, on the same farm or ranch—to provide

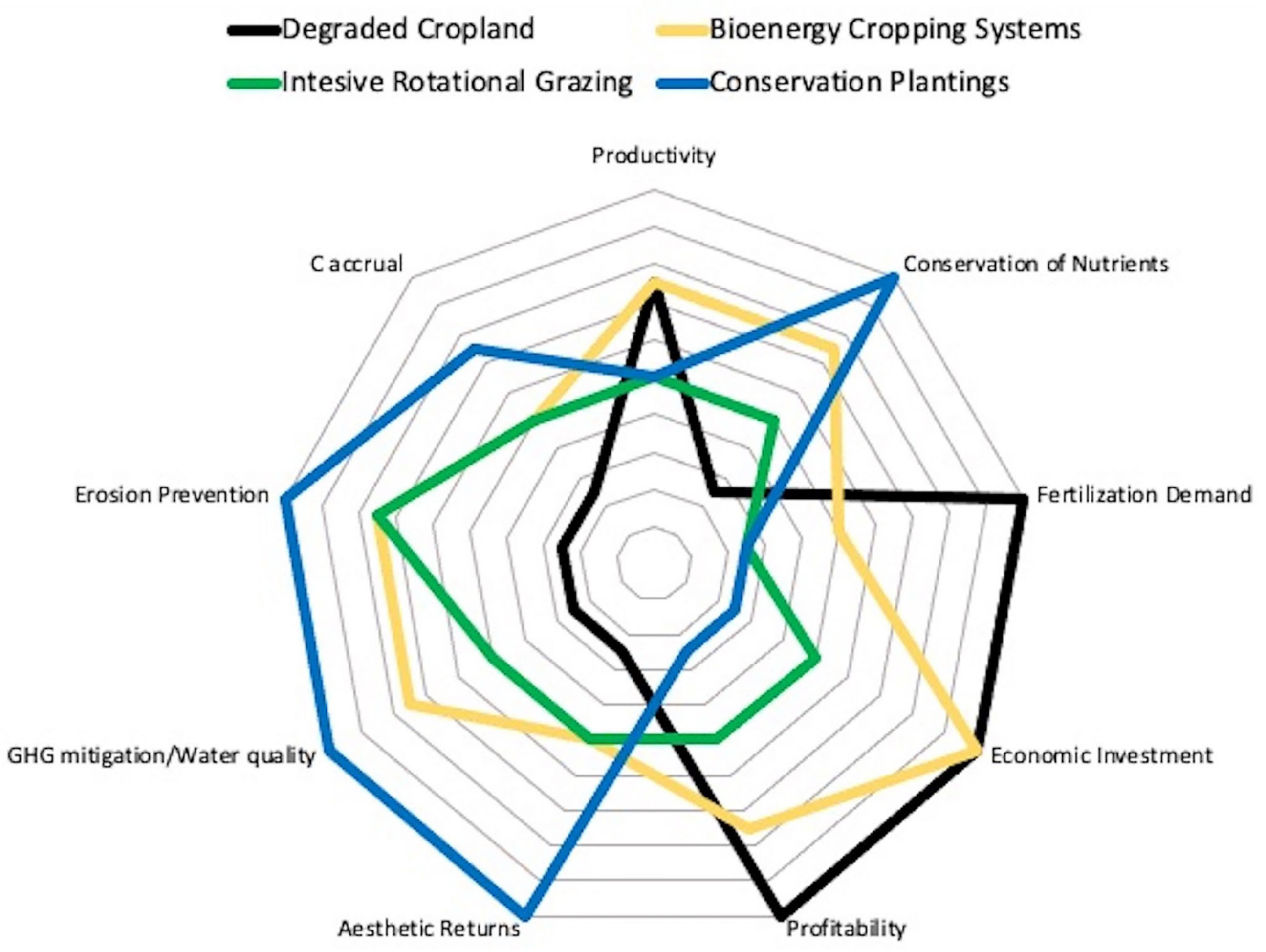

FIGURE 2 | Alternative combinations of ecosystem services that might be provided by different perennial systems as compared to degraded cropland.

the multifunctionality often sought in sustainable agriculture (Robertson and Harwood, 2001; Boody et al., 2005). Many other opportunities for restoration of soil fertility through perennialization are equally feasible. Some noteworthy examples include perennial grain systems (e.g., Glover et al., 2010; DeHaan et al., 2020), orchard and agroforestry systems (e.g., Subler and Uhl, 1990; Palm, 1995), and long cash crop rotations that include several years of perennial forage or cover crops. All have great potential to restore soil fertility on degraded lands.

Bioenergy Cropping Systems

Cellulosic bioenergy is central to all IPCC mitigation pathways capable of keeping end-of-century global temperature change below 1.5°C (Intergovernmental Panel on Climate Change, 2018), whether bioenergy is used for liquid fuel or electricity generation, or both. While some cellulosic feedstocks will come from agricultural and industrial by-products, a substantial fraction must come from purpose-grown biomass crops, mainly perennial grasses and short-rotation trees (Robertson et al., 2017). The amount of purpose-grown biomass required to meet C-negative energy demands is substantial—in the U.S. alone, at least a billion tons per year (U.S. Department of Energy, 2011) and globally much more (Nakada et al., 2014; Calvin et al., 2019).

Productive cropland cannot be used to sustainably meet much of this demand—converting lands now used to produce food to produce bioenergy will create pressure to convert other lands now unmanaged to food production in order to make up lost food crop productivity, negating much of the climate benefit of biomass crops on contemporary cropland. So-called indirect land-use change (ILUC) effects can only be avoided with unrealistic cropland productivity increases (to compensate for food production when arable cropland is planted to new bioenergy crops), or by avoiding altogether the use of current cropland for bioenergy (Robertson et al., 2017). On the other hand, the use of unproductive or degraded cropland for perennial bioenergy crops will have little ILUC impact on account of the additional climate benefit of removing these lands from annual crop production, and thus are also excellent candidate lands for perennial feedstock production.

Using degraded lands worldwide for cellulosic bioenergy production is thus attractive on two fronts. First, it avoids ILUC effects to allow the full climate benefits of cellulosic bioenergy to be applied toward climate mitigation without benefits' having to be discounted for the additional greenhouse gases produced when natural areas elsewhere are converted to food production. This also addresses targets from Sustainable Development goal 13, relating to climate action. Second, it provides a means whereby degraded lands can be restored to a more fertile state, allowing a greater productive capacity to progressively reduce the amount of land needed for bioenergy production, which in turn will allow these lands to return eventually to a more robust natural state to support global biodiversity goals (IPBES, 2019) or returned to food crop production to meet Sustainable Development goal 2 related to hunger. A growing proportion of bioenergy lands with restored soil fertility would be available for food production once global temperatures stabilized sometime after 2,100.

The restoration of soil fertility under perennial bioenergy crops draws on most of the mechanisms related to ecological nutrient management identified in Section Impacts of perennialization on fertility restoration: soil C accretion, N conservation, and more efficient P cycling. We know most about soil C accretion because of its importance to the climate benefit of bioenergy crops. N is important both because of its positive impact on biomass production but also its negative potential to further burden the biosphere's reactive N load and to discount the climate benefit of bioenergy production via fertilizer and nitrous oxide production. Phosphorus can also limit biomass production, especially in highly weathered tropical soils.

As noted earlier, soil C gains under perennial crops, whether grasses such as switchgrass (*Panicum virgatum*) or short-rotation trees such as hybrid poplar (*Populus* spp.), or even complex semi-natural communities such as restored prairie (Tilman et al., 2006; Gelfand et al., 2020), derived from root biomass and stabilized soil C. More specifically, these soil C gains are derived from root exudates and decomposition products in a soil physical environment conducive to the persistence of stable forms of soil C—in particular, C associated with aggregates (e.g., Tiemann and Grandy, 2015) and mineral surfaces (e.g., Garten and Wullschleger, 2000). Some have also advocated biochar additions to bioenergy crops, though the climate benefit will likely be less than were the biomass C instead fully converted to energy production in order to offset fossil fuel use (Paustian et al., 2016).

That soil C can accumulate under bioenergy crops even when all aboveground biomass is harvested illustrates the importance of roots as sources of stabilized soil C. Perennial legumes grown as forage crops have long been known to sequester soil C. In southwest Michigan USA, for example, Syswerda et al. (2011) showed that a continuous alfalfa stand harvested 3–4 times per growing season gained 1.0 Mg C ha^{-1} yr^{-1} in the Ap horizon its first 12 years, as others have documented (e.g., Kumar et al., 2018), and at almost three times this rate (2.9 Mg C ha^{-1} yr^{-1}) when considering the whole profile to 1 m. Soil C also accumulates but often more slowly under grasses; Schmer et al. (2011), for example, documented rates of SOC gain between 1.4 and 3.3 Mg C ha yr^{-1} to 1.2 m depth in a 5 year study of harvested switchgrass fields on farms in Nebraska, USA. Others (e.g., Frank et al., 2004; Chimento et al., 2016) but not all (e.g., Sprunger and Robertson, 2018) have found gains of a similar magnitude soon after switchgrass establishment. Soil C also accumulates under short-rotation tree crops (Chimento et al., 2016), although post-harvest SOC losses can substantially discount soil C gains when the soil is exposed to erosion and moisture and temperature conditions that accelerate decomposition when the soil is exposed prior to canopy closure of the next crop (Syswerda et al., 2011).

The two greatest risks of large-scale bioenergy production—apart from the use of contemporary cropland now used for food—are further biodiversity loss upon conversion of inappropriate land covers and further N loading of the biosphere. The use of appropriate crops on degraded lands minimizes both risks. First, use of the 864–951 million ha of abandoned cropland worldwide (Campbell et al., 2008; see Introduction) avoids lands of conservation interest—wetlands, old-growth forests, and other natural areas important for biodiversity conservation (IPBES, 2019). Avoiding land with significant forest cover is particularly important in order to avoid long-term C debt that works against climate benefits (Robertson et al., 2017); lands undergoing reforestation are already contributing to climate change mitigation (Griscom et al., 2017). Finally, planting native grasses and short-rotation trees that are native to a region will improve the conservation value of most degraded lands, typically dominated by non-native invasive species with less biodiversity value. Native mixed-species plantings should have an even greater benefit (Werling et al., 2014).

Second, avoiding crops with high N requirements or low N use efficiencies will keep additional reactive N from the environment. Non-leguminous biomass crops such as perennial grasses and short-rotation trees have low N requirements and high N use efficiencies, and if harvested post-senescence, will remove relatively little N in harvest. Mechanisms in section Impacts of perennialization on fertility restoration—in particular, persistent roots that occupy a large proportion of the available soil volume, pre-harvest translocation of N from aboveground biomass to roots, and relatively little N allocated to reproductive biomass such as seeds, resulting in high C:N ratios at harvest—creates a relatively closed ecosystem N cycle. This is even more the case when planting species capable of acquiring most or all of their own N through BNF (see section Nitrogen conservation). Empirical evidence for low N losses from perennial biomass cropping systems is accumulating (e.g., Ruan et al., 2016; Hussain et al., 2019), as is the potential for associative N fixation (Roley et al., 2019, 2020). Moreover, planting perennial biomass crops for biodiversity conservation or bioenergy or both in low-performing, unprofitable subfield portions of existing cropland (Schulte et al., 2017; Brandes et al., 2018) could avoid a substantial amount of contemporary N loss from this cropland (Basso et al., 2019).

All told, then, growing perennial biofuel crops on degraded lands could provide substantial climate mitigation while restoring long-term soil fertility. Non-leguminous perennial crops are especially attractive: few management inputs, long-term soil organic matter accretion, and N and P conservation with biodiversity and other co-benefits. The growth of bioenergy markets—currently unrealized—could make such practices economically profitable as well, providing a well-rounded suite of ecosystem services (**Figure 2**).

Intensive Rotational Grazing

Managing perennial forage as pastures for grazing provides a second major management system for restoring degraded lands. In contrast to current grazing practices that tend to maintain or further exacerbate degraded soils, often due to overgrazing, here we refer to grazing management that aims to maintain perennial forage production in a sustainable way by rotating animals across the landscape. Rotational grazing can take many different forms. Simple rotational grazing (RG) moves animals at low intensities with 2–14 pastures per herd (Briske et al., 2011; Roche et al., 2015). Management intensive grazing (MiG) moves animals at higher intensities with 16+ pastures per herd, and adaptive multi-paddock grazing (AMP) often includes 40+ pastures per herd (Teague et al., 2015; Barton et al., 2020; Mosier et al., 2021). Low intensity systems tend to have more fixed, planned animal movements, whereas more intensive systems are more flexible and tend to move the animals based on forage growth (Undersander et al., 2002). By rotating the animals, the soil and perennial vegetation are provided grazing-free periods that help to maintain and improve soil fertility and perennial productivity (Kemp et al., 2000).

Pastures containing diverse, perennial vegetation offer forage that can often be more productive (Minns et al., 2001; Moore et al., 2004; Skinner et al., 2004) and available for a greater proportion of the growing season (Ferchaud et al., 2016) compared to grazing systems that rely heavily on annually planted crops for year-round forage. Increased productivity of grazed perennial forage could also be due to the increased drought and stress tolerance of many perennial grasses (Tilman and Downing, 1994; Skinner et al., 2006). Additionally, in perennial pastures, there are no annual tillage or extreme harvest events, so more above- and belowground biomass remains after grazing events, especially in AMP grazing systems, which aim to leave 50% of forage uneaten (Teague et al., 2013). With higher productivity of perennial forage, these lands are able to support more animals with increased stocking rates without the negative effects of overgrazing (Jakoby et al., 2015; Teague et al., 2015). Perennialization also diversifies the vegetation available for grazing, often producing more nutritional forage and improving cattle health (Teague et al., 2016).

There are many examples of improved soil fertility from perennial pastures that are rotationally grazed. When the perennial pastures are grazed, the animals keep nutrient cycles more closed and thus conservative, and as well-inexpensive—manure generated on-site provides organic C, N, and P inputs that can improve nutrient retention and availability (Elser and Bennett, 2011; Mosier et al., 2021). In AMP grazing systems, the use of fertilizers and other inputs is minimized or even eliminated; for example, Mosier et al. (2021) found that unfertilized AMP pastures had more soil N than non-AMP pastures annually fertilized. Rotationally grazed perennial systems have also been shown to improve soil health across physical, chemical, and biological indicators (Teague et al., 2011; Byrnes et al., 2018), also resulting in improved water retention and infiltration (McCallum et al., 2004; Teague et al., 2011). The recovery of degraded land using perennial pastures that are rotationally grazed has been shown in both humid regions such as the southern U.S. (Machmuller et al., 2015; Mosier et al., 2021) as well as in semi-arid rangelands in Africa and the western United States (Teague and Dowhower, 2003; Badini et al., 2007; McDonald et al., 2019).

In addition to soil fertility benefits, rotational grazing in perennial pastures can also reduce some greenhouse gas emissions. Teague et al. (2016) found that grazed systems with year-long grass cover produced a smaller greenhouse gas footprint than croplands with periods of bare soil through increased soil C accrual. Further reductions in greenhouse gas emissions, specifically methane, can be achieved through AMP grazing. For example, Shrestha et al. (2020) found that AMP grazing systems increased methane uptake 1.5× compared to other grazing systems. Rotationally grazed perennial systems can also reduce the total amount of CO_2 emissions associated with production as compared to other conventionally grazing systems through increased C sequestration and reduced external forage requirements (Bosch et al., 2008). However, some studies have found that N_2O emissions were increased in these rotational systems due to higher stocking rates, though these emissions were offset by higher levels of soil C accretion (Bosch et al., 2008; Rowntree et al., 2020). Reductions in net greenhouse gas emissions will also address Sustainable Development Goals linked to climate action.

The costs associated with converting degraded croplands into perennial forage systems that are rotationally grazed, such as the need for more fencing, are relatively low and readily offset by increased productivity and economic returns (Teague et al., 2013; Jakoby et al., 2015; Wang et al., 2018), as demonstrated for areas in the Midwest United States (Riley et al., 1997). Additionally, with higher perennial productivity and longer growing seasons, animals in these systems become less reliant on external sources of forage (Wang et al., 2018), another cost savings. And particularly in dry environments, conversion from underperforming croplands to perennial pastures that are grazed is attractive, especially when ranchers consider forecasted increases in drought intensity (Wang et al., 2021).

All told perennial pasture systems that utilize intensive rotational grazing have the potential to deliver an improved suite of ecosystem services relative to degraded grazing lands and underperforming cropland (**Figure 2**) while at the same time restoring soil fertility to provide an increasingly productive land base to meet future food needs. Increased productivity will also proportionately alleviate pressures to convert natural ungrazed areas to pastureland, providing significant indirect biodiversity benefits.

Conservation Plantings

At the low end of the perennial management intensity spectrum is the practice of converting degraded croplands into conservation plantings in order to restore soil fertility. Its simplest form is the fallow phase of bush-fallow or shifting cultivation agriculture—simply leaving the land to undergo ecological succession with its restoration of soil organic matter and nutrient availability, as noted earlier (section Introduction). In many cases today, however, soil degradation is past the point of rapid recovery, and the ubiquity of invasive plants means that the vegetation that recovers may bear little resemblance to the original native community with its associated biodiversity benefits. Often more direct conservation management is warranted, whereby specific species selections are made with the explicit goals of restoring ecosystem health or biodiversity or both.

An example of such a management program is the USDA Conservation Reserve Program (CRP) (Skold, 1989). Initiated as a set-aside program to create higher commodity prices—removing land from production creates higher prices by reducing supply—the program now targets environmentally vulnerable lands, otherwise subject to high erosion and nutrient losses, that can be converted to habitat for wildlife and provide other environmental benefits. In short, landowners are paid to take lands that are vulnerable to degradation out of production and to replace them with perennial systems that minimize soil erosion (U.S. Department of Agriculture, 2006) and improve soil health (Li et al., 2017), water quality, and wildlife habitat (Wu and Weber, 2012). An increasingly recognized benefit has been greenhouse gas mitigation (Farm Service Agency, 2011), achieved by increasing soil C sequestration and reducing the use of N fertilizers responsible for soil nitrous oxide emissions (Robertson, 2014), simultaneaously helping to reach Sustainable Development goal 13, which addresses climate change and its impacts.

By 2011 the CRP had reduced the use of N and P fertilizers by 275 and 55 million kg, respectively (Farm Service Agency, 2011), and between 1986 and 2014 resulted in avoidance of over 7 billion Mg of soil erosion (Stubbs, 2014). Earlier studies estimated that CRP enrollment had an average erosion savings of 38 Mg ha^{-1} (Ribaudo et al., 1990). Young and Osborn (1990) valued the reduction in wind erosion at up to a billion $US, and Ribaudo et al. (1990) valued downstream water quality improvements (from avoided water erosion and nutrient losses) at several times this amount.

Effects of converting cultivated land to conservation lands like CRP have increased soil C and N stocks appreciably. In the U.S., Burke et al. (1995) showed CRP improvements in soil stability and fertility that accompanied soil C and N accretion. Improvements can occur quickly, often after only 5 years, likely due to higher plant productivity from a diversity of seeded perennial grasses (Gebhart et al., 1994; Reeder et al., 1998; Baer et al., 2000). On the other hand, recovery rates can vary by physiochemical soil condition and as well-depend on past land use and disturbance history (Post and Kwon, 2000). In particular, recovery can be slower in climate regions with lower plant productivity, such as arid regions of the western United States (Robles and Burke, 1998).

Similar trends of soil C recovery have been reported for conservation plantings in Europe and Asia. In Germany, Breuer et al. (2006) showed greater soil C and N stores in sites converted to perennial grassland species than in sites under continuous cropland. In Russia and China, several authors have shown a high potential for soil C stock recovery in croplands returned to native grass vegetation. Soil C accretion rates for restored grasslands in Russia were nearly 50% higher than for forests in the same region (Shvidenko and Nilsson, 2003; Vuichard et al., 2008). Similarly, on the Chinese Loess Plateau, abandoned croplands converted to grasslands sequestered more soil C than did restored forested lands (Wei et al., 2012; Jin et al., 2014). Zhang and Shao (2018) also measured higher soil N, P, and overall soil fertility after maize and wheat croplands were converted to perennial grassland.

Conversion of degraded land to conservation plantings benefits multiple taxa, including those that constitute soil microbial communities. Matamala et al. (2008), for example, showed microbial community recovery in a restored prairie converted from cropland, although the recovery was at a much slower rate than soil C and N stocks. Similarly, Baer et al. (2000) showed a slow but consistent increase in microbial biomass on CRP lands planted to native perennial grasses. In China's Loess Plateau, Zhang et al. (2012) documented increases in microbial species richness and biomass, as well as enhanced microbial activity, after cropland conversion to perennial grassland. Most authors relate recovery to perennial rooting systems and associated increases in C inputs from root turnover and exudation.

With the exception of direct economic return or food production, the ecosystem services delivered by conservation plantings are considerable (**Figure 2**). Removing land from production and its associated inputs immediately eliminates many of the environmental costs of agriculture and initiates the restoration of supporting services such as biodiversity and soil fertility and regulating services such as flood control. However, it also eliminates most provisioning services, which means the direct economic returns derived from food, fiber, or fuel production. That said, with the potential for ecosystem service payments (Swinton et al., 2007) that may include payment for biodiversity benefits such as pollination and natural pest suppression (Asbjornsen et al., 2013; Landis and Gage, 2015), direct economic returns may become an additional ecosystem service provided by conservation plantings (**Figure 2**). Ultimately, of course, the repatriation of these lands to food production will benefit future food security as once-degraded lands regain their capacity to produce food crops.

Return to Food Production After Soil Fertility Restoration With Perennials

To break the cycle of degradation—recovery must be a key part of any soil restoration initiative. It makes little sense to invest decades in management that restores the productive capacity of a system—whether by bioenergy production, intensive rotational grazing, conservation plantings, or any of a number of other practices—only to allow the system to degrade again when returned to food production. Thus, the production system implemented post-recovery must be sustainable. Sustainable Development Goal 2 embodies this challenge: to ensure sustainable food production systems and implement resilient agricultural practices that increase productivity and production; that help maintain ecosystems, strengthen the capacity for adaptation to climate change, extreme weather, drought, flooding, and other disasters; and that progressively improve land and soil quality.

This is a tall order consistent with the need to incorporate sustainable practices on lands that are not currently degraded (see other papers in this Collection). The principles outlined in section Impacts of perennialization on fertility restoration apply. To sustain fertility will require practices that incorporate ecological nutrient management, drawing on principles from organic and regenerative agriculture to maintain stable SOC stores and link C, N, and P cycles to provide nutrients with little environmental loss. First and most important is the need to diversify rotations. Complex rotations that include perennial crops for forage or fallow have, for reasons described earlier, nutrient cycles that are more efficient than simpler rotations. Agricultural systems export C, N, P, and other elements with harvest, so they will never have closed cycles, but high system-wide nutrient use efficiency is achievable with continuous green cover and crops that fix N and mobilize plant-available P. Within-crop diversity can also help to build and maintain greater stabilized C stores and improve nutrient use efficiency, both by intercropping and by using mixed-species cover crops and forages.

Other practices that will be important to engage include no-till to better maintain soil health; variable rate nutrient management and subfield conservation plantings to avoid over-fertilizing low yielding areas of a given field; minimal, precisely targeted pesticide use in order to keep soil food webs intact and fully functional; and animal integration via periodic grazing or manure return. If perennial grains become agronomically viable in the coming decades, a new path will open to incorporate perennial crops into cereal croplands. Incorporating perennials into post-recovery rotations is thus a key aspect of sustainable, regenerative soil management.

BARRIERS TO ADOPTION

Farmers and landowners have numerous options for incorporating perennials into their production and land management strategies, ranging from more complex crop rotations that include perennial crops such as forage grasses and legumes (King and Blesh, 2018) to the establishment of perennial cropping systems such as those for cellulosic bioenergy, rotational grazing, and conservation plantings noted above. Why aren't these practices more widely adopted? Barriers are not, in general, related to knowledge gaps—we have the fundamental knowledge to deploy restorative perennial cropping systems today, and most farmers have the knowledge and skill to successfully establish and manage them. Rather, barriers are largely socioeconomic, related to global trade and national policies that reward the status quo. Three barriers, in particular, stand out.

First is the continued pressure of global food demand. Global food needs are expected to continue their upward trajectory; projections of 30–50% greater food needs by mid-century on account of population and income growth (Food Security Information Network, 2017) will exert continuous pressure on farmers to intensify and expand food production. To the extent that expanded production cannot be met by intensification, there will be pressure to utilize for food production degraded lands with their inherent production and nutrient conservation limitations.

Second are policies that reinforce and reward annual cropping on degraded farmland. In the United States, crop insurance incentivizes farming on even unprofitable cropland as farmers are compensated for poor annual yields—which occur ever more frequently on such lands, creating a downward spiral of positive feedbacks. Moreover, crop insurance in the U.S. and subsidies elsewhere do not incentivize ecological management and are in any case available for only a select few commodities, directly discouraging crop diversity (Archer et al., 2003) and instead rewarding low diversity, high input production systems. As noted by Pascual and Perrings (2007), there is no global market for soil fertility or cropland diversification, and with current policies creating financial roadblocks that discourage regenerative practices, land abandonment is too often the eventual result.

A final major barrier is the lack of markets for some of the most promising restorative perennial cropping systems. In the examples above, neither cellulosic bioenergy crops nor conservation plantings have contemporary markets, nor are regional markets for diverse grain crops sufficiently available—even in the U.S. Midwest, crops as common as canola (*Brassica rapa*) cannot be grown for lack of nearby processing plants. Thus, not only are there often disincentives for moving away from degraded farmland but there are also no immediate incentives—and indeed disincentives—for adopting regenerative practices.

Two solutions seem tenable, especially in more affluent countries: removing perverse incentives that motivate land degradation and paying farmers for the delivery of ecosystem services (Robertson et al., 2014). By expanding crop subsidy payments, whether direct or indirect, to include additional annual and perennial crops, producers could be rewarded for the management of crop diversity for ecological nutrient management and the accompanying soil restoration. Co-benefits of diversification include resilience to extreme weather (e.g., Bowles et al., 2020), a more stabilized food supply (e.g., Renard and Tilman, 2019), and avoiding yield penalties associated with continuous rotations (Seifert et al., 2017).

Second, payments for ecosystem services (e.g., Swinton et al., 2007) provide a means for society to directly compensate landowners and operators for agricultural practices they would otherwise not adopt. Long lists of candidate services have been generated, and nascent markets are paying farmers for soil C sequestration (Climate Action Reserve, 2020) and more precise N management (Millar et al., 2012), though payments are currently insufficient to motivate much adoption. But payments for climate mitigation practices have been recently proposed in the U.S. and may allow incentives for sequestering soil C using more diverse cropping practices that include perennial crops. Likewise, the USDA CRP program could be expanded to accelerate C accretion in soil and biomass, and markets for cellulosic bioenergy may be on the horizon (Robertson et al., 2017). Ensuring that perennial crops remain a principal target for the delivery of these services will allow the full restorative benefits of perennialization to be realized.

CONCLUSIONS

There is an abundance of degraded land in the world in need of soil fertility restoration to meet current and future food security needs. Using perennialization to restore lost fertility seems possible through practices that promote C accretion and the efficient use and conservation of N and P. Carbon accretion is central to fertility restoration, resulting from greater amounts and diversity of belowground C inputs, improved soil structure, and less soil disturbance. Nitrogen conservation can result from practices that improve system-wide N use efficiency, including perennials with their ability to capture N from deeper in the soil profile, translocate N to roots prior to senescence, and for some, fix atmospheric N. Improved P retention and recycling in perennials arises from enhanced inputs of root and microbial metabolites that make soil mineral and organic P available for plant uptake, and fewer losses via runoff, leaching, and erosion.

Barriers to using perennialization to restore degraded soils are surmountable with policies that can incentivize landowners, farmers, and ranchers to manage ecological processes for soil fertility and ecosystem services, perhaps by shifting incentives away from land degrading practices such as intensive short rotation grains toward more diverse rotations and other practices related to regenerative agriculture. Ultimately millions of ha of currently degraded crop and rangeland could be repatriated to restore and enhance ecosystem services, including those related to biodiversity, water, and nutrient conservation, and economic and societal well-being.

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All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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Belowground Dynamics Influence Nitrogen Cycling and Crop Productivity in Diversified Corn Systems

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Ecological nutrient management is a strategy that can help create resilient cropping systems and reduce the negative impact that agricultural systems have on the environment. Ecological nutrient management enhances plant-soil-microbial interactions and optimizes crop production while providing key ecosystem services. Incorporating perennial legumes into crop rotations and implementing no-till to enhance organic nitrogen (N) soil pools could reduce the need for inorganic N fertilizer inputs and lead to improved soil health. Plant and soil N pools need to be further quantified to understand how to enhance soil health across a range of agroecosystems. This paper aims to quantify plant and soil N pools in systems contrasting in crop perenniality (corn–corn, corn–soy, and corn–forage–forage) and tillage intensity (chisel till vs. no-till). Key plant, soil, and organismal metrics of N cycling were measured including fine root production, N-Acetyl-B-Gulcosaminidase (NAG) enzyme activity, and soil protein, nematode enrichment opportunist (fungal and bacterial feeding nematodes) and the nematode Enrichment Index. Fine root production was determined using in-growth mesh cores. Findings reveal that monoculture cropping systems with reduced tillage intensity and rotations with perennial legumes had significantly greater fine root N (FRN), soil protein and NAG enzyme activity ($p < 0.05$) relative to corn-soy. Additionally, nematode bacterivore enrichment opportunists ($b1$) were significantly reduced in corn-corn systems when compared to all other crop rotation systems. Correlation analyses indicated positive and significant relationships between FRN and soil protein ($p < 0.05$). These results demonstrate that lengthening crop rotations with perennial legumes and incorporating no-till management can increase organic N inputs, N mineralization rates, and organic N storage. Such ecological approaches to management have the potential to reduce the need for inorganic N inputs, while increasing long-term soil health and crop productivity.

Keywords: roots, soil health, nematodes, ecological nutrient management, perennial agroecosystems

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INTRODUCTION

The conventional approach to nutrient management is to apply inorganic sources of nitrogen fertilizer to ensure rapid crop nutrient uptake that maximizes crop yields. Typically, crops can only take up between one-third to one-half of the fertilizer that is applied (Robertson and Vitousek, 2009; Conant et al., 2017). The remaining fertilizer is generally lost to the environment contributing to eutrophication and global climate change (Robertson and Vitousek, 2009; Billen et al., 2013). In contrast, ecological nutrient management practices aim to optimize crop productivity while simultaneously enhancing soil fertility and long-term ecosystem sustainability (Drinkwater and Snapp, 2007a).

While there are numerous definitions and approaches to ecological nutrient management, here we define it as a form of management that seeks to foster plant-soil-microbial interactions that optimize crop production and simultaneously provide ecosystem services such as improved soil health and nutrient retention. In contrast, we classify conventional systems as those that depend on the use of inorganic nutrient additions and disruptive tillage practices to maintain yields. Ecological nutrient management provides a framework toward enhancing food production and increasing resilience, which is sorely needed due to accelerated population growth and climate change. The United Nations sustainability goals remind us that 8.2% of the world lives in extreme poverty and that 26.4% suffer from food insecurity (UN Sustainable Development Goals, 2020). Additionally, the effects of climate change continue to impact agricultural production around the world (Agovino et al., 2019). Thus, while access to safe and nutritious food must increase, it is no longer feasible to approach agriculture through the single lens of maximizing crop production. Ecological nutrient management could serve as a sustainable solution to food production around the world and serve as an effective way to reach the United Nations Sustainability Goal 2.4, which seeks to ensure sustainable food production and resilient agricultural practices that not only enhance crop production but also help to maintain ecosystems that strengthen the capacity for climate adaptation and improved soil quality (UN Sustainable Development Goals, 2020).

However, questions remain on the best ways to quantify nutrient pools, especially under the umbrella of Ecological Nutrient Management, which is essential for understanding which agroecosystems are most effective at boosting yields while enhancing soil health. Furthermore, the improvement of nutrient pools that contribute to soil health and long-term sustainability is essential for building resilient agroecosystems. The conventional model for managing nutrients within agricultural systems focuses solely on inorganic nutrient pools, inhibiting nitrification and dentification, and fertilizing to match crop N uptake (Drinkwater and Snapp, 2007a). However, these management strategies have been shown to produce unsustainable yields, develop systems that cannot withstand stressful conditions, and promote nutrient leaching and run-off (Syswerda et al., 2012; Jungers et al., 2019). Management strategies that encompass an ecological approach may provide a solution through shifting the focus to enhancing rhizosphere interactions. Specifically, management strategies than can maintain nutrient reservoirs for plant access, promote both organic and inorganic nutrient pools, enhance microbial mineralization, and reduce the size of inorganic nutrient pools have the potential to increase ecosystem resilience (Drinkwater and Snapp, 2007a). Crop diversification is one agricultural management practice that fits well within the ecological nutrient framework because it has been shown to maximize nutrient assimilation and produce increased yields under climatic stress (Bowles et al., 2020). However, the specific interactions between plant and soil nutrient pools within systems of varying crop diversity have yet to be quantified. In addition, reduced tillage intensity is another management practice that fosters and ecological approach. Specifically, no-till systems can enhance nutrient reservoirs for plant-uptake through greater aggregation caused by reduced mechanical disturbance (Jiao et al., 2006).

There have long been attempts to assess ecological nutrient management within the rhizosphere to gain a deeper understanding of how belowground processes can support crop productivity (Drinkwater and Snapp, 2007b; Zhang et al., 2017a). That said, these reviews have approached rhizosphere dynamics largely from the standpoint of which management practices can best increase rhizosphere processes and have been vague on the best ways in which to accurately quantify organic nutrient pools, such as the organic nitrogen (N) pool. In truth, advancements in soil health methodologies in recent years have helped bolster our understanding of nitrogen cycling within the rhizosphere (Moebius-Clune et al., 2008; Hurisso et al., 2018b).

For instance, fine root production plays a vital role in rhizosphere dynamics through maintaining organic N pools. Specifically, fine roots serve as a large source of N within rhizosphere systems and the fast turnover of fine roots can allow for N retention (Gordon and Jackson, 2000; Sprunger et al., 2018). Furthermore, the N supply provided by fine roots is essential for plant biogeochemical functions and can stimulate microbial growth and enhance N mineralization and the release of soluble N that can be used for plant growth within the rhizosphere (Gordon and Jackson, 2000; Jackson, 2000). Ecological nutrient management practices such as perenniality, have also been shown to produce a greater pool of fine root N relative to annual root systems (Dietzel et al., 2015; Sprunger et al., 2018). Moreover, the extensive root systems of perennial crops also allows for a greater N use efficiency (Sprunger et al., 2018). Therefore, diversifying cropping systems using perennial crops may enhance N sinks that can contribute to plant–microbe–soil N cycling and reduce the need for N fertilizer additions (Crews and Peoples, 2005; Dawson et al., 2008; Sprunger et al., 2018).

Quantifying soil N in agricultural systems is challenging as these pools constantly change over the course of a growing season. Moreover, when soil N is tested, most metrics only measure the inorganic forms of N. This leaves several key N pools unquantified, including the organic pool of N a key component of soil organic matter (Hurisso et al., 2018a). While other tests have been developed to measure important fluxes on soil N, including mineralizable N and potentially mineralizable N incubations, these tests still do a poor job of reflecting biologically available pools of N (Hurisso et al., 2018b). Recent efforts have led to the development of soil protein, which is a rapid soil health indicator that can effectively quantify the primary pool of organically bound N in soil (Hurisso et al., 2018b). Soil protein is a sensitive soil health indicator that can detect differences across a wide range of agroecosystems and has been shown to be strongly correlated with maize yields (Roper et al., 2017; Sprunger et al., 2018, 2020). In addition to soil protein, the rate of N mineralization in soil systems can function as an indicator of the quality of organic matter deposits and the rate of nutrient availability for plant use in soil systems. Enzyme activity of N-Acetyl-B-Glucosaminidase (NAG) can also serve as an important measure N mineralization within a system, as well as represent the functional capacity of soil microbial communities.

A major principle of ecological nutrient management is to assess dynamic interactions between organisms and their environment. Quantifying certain microfauna, such as nematode communities, presents an opportunity to not only understand community structure but also ecological function (Laakso et al., 2000; Ferris et al., 2001; Yeates, 2003). Since nematodes range in trophic complexity, they can provide insight into nitrogen cycling (Ferris, 2010). Specifically, bacterial feeders and fungal feeders that are in entry level decomposition channels (colonizer-persister groups 1 and 2), respond rapidly to influxes of resources because of their short life-cycles, and thus benefit more from resource subsidy (Bongers, 1990; Zhang et al., 2017b). Furthermore, bacterivore and fungivore nematodes prey on primary decomposers and can alter the mineralization rates of nutrients needed for plant growth. N mineralization rates can be significantly affected by bacterivore and fungivore grazing as they excrete NH_4^+ and spread bacteria and fungi through the soil (Ingham et al., 1985; Chen and Ferris, 1999; Okada and Ferris, 2001). Thus, quantifying the abundances of enrichment opportunist bacterivores ($b1$) and fungivores ($f2$) can indicate N mineralization throughout the soil food web (DuPont et al., 2009).

Here we seek to assess crop productivity and soil health by quantifying key above and belowground N pools in systems that have been managed conventionally vs. ecologically for almost six decades. The trial consists of conventionally managed systems that use chisel tillage and monoculture crops such as continuous corn (*Zea mays*) and ecological nutrient based systems that include corn rotated with perennial legumes under no-till. The specific objectives are to (1) evaluate N cycling in agroecosystems contrasting in crop rotational diversity and tillage intensity by quantifying plant and soil organic pools of N. (2) Investigate the relationship between nitrogen pools and crop productivity across all systems.

MATERIALS AND METHODS

Site Description

This study took place at The Northwest Crop Rotation Trial of The Ohio State University (established 1963). The Northwest Crop Rotation hereafter referred to as Hoytville, is located at Custar Wood County, OH at 41°13′N, 83°45′W. The Northwest soil series is a Hoytville Clay Loam and the taxonomic class is a fine, illitic mesic Mollic Epiaqualf. The site is a deep poorly drained soil with a slope range of 0–1% with high shrink swell potential.

Experimental Design

The site is arranged as a full factorial, randomized complete block design, with three blocks and plots being 30.5 × 6.4 m. The tillage treatment consisted of two different tillage intensities: no-till (NT) and chisel till (CT). No-till is zero tillage with the residue of the previous year left on the field. In contrast, chisel till is performed in the spring with 30% of the residue from the previous crop, where the soil is disturbed down to 12 cm. The crop rotation treatment consisted of three levels: corn–corn (*Zea mays*); corn–soybean (*Glycine max*) (CS); and a corn–forage–forage (CFF) rotation. The corn was planted in first half of June 2020. For the first 55 years of the experiment, the forage crop in the CFF system consisted of alfalfa (*Medicago sativa*). However, in 2019, the cropping system changed to include a mix of oats (*Avena sativa)* and red clover (*Trifolium pretense),* where the forage system was harvested once in October previous to planting with corn the following spring. This entire study was conducted during the corn phase of each rotation. All corn plots regardless of tillage and crop rotation were fertilized with urea (34–45 kg ha^{-1}) during corn pre-planting in the Spring. Additionally, N fertilizer was added during the V5 corn stage (202 kg ha^{-1}). Phosphorus and potassium was applied depending on soil test results. In 2020, the seeding rate for corn was ∼84,014 seeds ha^{-1}.

Aboveground Biomass

Three whole corn plants were randomly collected from each corn plot 2 weeks before grain was removed in October, 2020. The stalk and grain were dried and weighed. Next, the stalk was chipped, and subsamples for each plot were then collected and analyzed for N content using a Costech ECS 2010 CHNSO elemental analyzer. Aboveground biomass (kg/ha^{-1}) (ABB) was calculated by multiplying the weight of one plant by the number of plants per hectare (Equation 1). Aboveground N (kg ha^{-1}) (ABN) and was calculated by multiplying the ABB with the concentration of N (g kg^{-1}).

$$\text{ABB} = (\text{weight of 1 plant kg}) \times (84,014 \text{ plants/ha}) \tag{1}$$

Fine Root Biomass

Three ingrowth mesh cores were placed into each corn plot 2 weeks post corn emergence to measure the fine root biomass produced by the corn plant during the current growing season (Ontl et al., 2013; Sprunger et al., 2017). In certain cropping systems, ingrowth mesh cores have been found to overestimate fine root biomass, that said, such ingrowth mesh cores are still an excellent method for quantifying fine roots and comparing system level differences (Ontl et al., 2013). Ingrowth cores were made from plastic mesh with a hole size of 2 mm. The plastic mesh was stapled to form a cylinder of 5 cm in diameter × 13 cm long and the bottom was closed with a plastic cap. Soil cores were taken with hammer probes that had the same cylinder length as the mesh plastic cores. Soil was sieved to 4 mm and sand was then added in a 3:1 volume based soil to sand ratio. Ingrowth mesh cores were then filled and placed upright into the

5 cm dimeter × 13 cm depth holes. Stratified random sampling was used in which two ingrowth mesh cores were placed 1.9 cm from the harvest rows and one ingrowth mesh core was placed within one of the harvest rows on each plot in the given site. The ingrowth mesh cores were extracted at the same time as the aboveground biomass. Ingrowth mesh cores were extracted next to the whole corn plants that were collected for aboveground biomass 2 weeks before grain was removed in October 2020. After extraction cores were refrigerated (4°C) until processing. Corn fine roots were processed by a hydropneumatic elutriation and were washed free of soil over a 1 mm sieve. Fine root biomass (FRB) was dried at 60°C for 48 h, weighed, ground to a powder with a mortar and pestle for determination of N concentrations using a CN Elemental Analyzer (Elementar Americas; Mt. Laurel, NJ). Fine root biomass (kg ha^{-1}) was calculated as the fine root core biomass (B) divided by the core area (CA) multiplied by 10,000 cm^2/m^2 (Equation 2). Fine root N (kg ha^{-1}) (FRN) was calculated by multiplying the FRB (kg ha^{-1}) with the concentration of N (g kg^{-1}).

$$\mathrm{FRB} = 10,000\mathrm{cm}^2/\mathrm{m}^2 \times (\frac{\mathrm{B}}{\mathrm{CA}}) \tag{2}$$

Soil Sampling

Soil samples were collected twice over the course of the growing season: 2 weeks post planting and just prior to corn harvest. Fifteen soil cores (1.9 cm diameter) were collected down to 10 cm in each plot to make one composite sample. Stratified random sampling was used to collect the soil, in which random soil samples were taken that encompassed the entire plot (Parsons, 2017). Soils were subsampled for elemental and nutrient analysis (5 g), soil moisture (45 g), soil texture (50 g), soil protein (40 g), and enzyme activity analysis (10 g).

Soil Property Analysis

Soils were sent to Spectrum Analytics (Washington Court House, OH) for elemental and nutrient analyses, which included organic matter and pH. Soil organic matter was determined via loss on ignition (Combs and Nathan, 1998). Soil moisture was determined using fresh soil (45 g), that was then dried at 105°C for 24 h, and finally weighed (**Supplementary Table 1**). Soil texture was assessed using the protocol adapted from (Gee and Bauder, 1986). In summary, the soil was separated into particle size of sand (0.05–2.00 mm), silt (0.002–0.05 mm), and clay (<0.002 mm) through determining the differences on settling rates by Stoke's Law. Soils were pretreated with sodium hexametaphosphate to enhance the separation and dispersion of soil aggregates and a hydrometer was used to measure the density of soil particles in suspension at specific periods of time.

Soil Protein Analysis

Soil protein, which measures the labile pool of N within the soil was determined using methods adapted from Hurisso et al. (2018b). Prior to analysis soils were air dried for 2 days immediately after sampling and on the third day samples were dried in a desiccator at 40°C for 24 h. After drying, samples were sieved and ground to 2 mm. Then, sodium citrate solution (24 ml) was added to the soil (3 g), shaken for 5 min, autoclaved for 30 min at 121°C, cooled for 40 mins, shaken for 30 mins, then the solution (1.5 ml) was transferred to a clean centrifuge tube and centrifuged for 3 mins. Soil protein was quantified using the colorimetric bicinchoninic-acid (BCA) assay (Thermo Scientific, Pierce, Rockford, IL) in a 96-well spectrophotometric plate reader at 562 nm.

Enzyme Sample Processing

N-Acetyl-β-Glucosaminidase (NAG) was measured using the protocol adapted from Tabatabai (1994) and Deng and Popova (2011). Prior to the analysis soils were sieved to 4 mm and refrigerated at 4°C until analyses was performed. Briefly, duplicates of soil (1 g) were placed within an Erlenmeyer flask and NAG Acetate buffer (4 ml) was added. Then 1 ml of p-nitrophenyl-N-Acetyl-β-D glucopyranoside substrate was added to each flask. The sample control was prepared through the same procedure, except no substrate was added to the flask. All samples were then incubated at 37°C for 1 h. After incubation 1 ml of 0.5 M $\mathrm{CaCl_2}$ and 4 ml [Tris (hydroxymethyl) aminomethane] THAM (pH 12) were added to terminate the reaction. Then, p-nitrophenyl-N-Acetyl-β-D glucopyranoside substrate (1 mL) was added to all control samples. The soil suspension was filtered, and the absorbance was measured at 415 nm. Enzyme activity was calculated using a calibration curve of standards containing 0, 100, 200, 300, 400, 500, 600, 700, 800, 900, or 1,000 nmol of *p*-nitrophenol.

Nematode Identification and Calculations

Free-living nematodes are soil microfauna which can detect changes in nutrient enrichment and thus indicate N cycling within varying systems. Free-living nematodes were extracted using the elutriation method (Oostenbrink, 1960). In summary, 100 cc of soil sample was soaked for 24 h, thoroughly stirred, passed through the elutriator, and the solution was collected in 50 ml centrifuge tubes. Next, the solution was processed using the centrifugal sugar flotation method (Hooper et al., 2005). The total number of nematodes were counted in each sample under a microscope at 50× magnification and 100 individuals were identified to family at 100–400×. If the sample contained <100 nematodes all individuals were identified. Nematode counts were expressed as the number of nematodes in each soil fraction (100 g of dry soil fraction). Each nematode was classified as an adult or juvenile to allow the determination of the population stage structure. Nematode taxa was assigned to trophic groups (Yeates, 2003) and functional guilds (Bongers and Bongers, 1998). The Enrichment Index (EI) was calculated using NINJA (Sieriebriennikov et al., 2014). The bacterial feeders cp-1 ($b1$) and fungal feeders cp-2 ($f2$) nematode groups were calculated through the sum of the abundance of all $b1$ or $f2$ of nematode feeding groups within each sample (DuPont et al., 2009).

Statistical Analysis

Normality of data was assessed through the use of studentized residuals plots with MASS in R (Venables and Ripley, 2002). For FRB, FRN, ABB, and ABN, a randomized complete block design Analysis of Variance (ANOVA) was conducted using the PROC MIXED procedure SAS v.9. Means separation was conducted

TABLE 1 | Organic matter mean and (SE) ($n = 3$), sand, silt, clay, and pH mean (SE) ($n = 3$) sampled in October 2020 from systems comparing three different crop rotations and two tillage intensities.

Rotation	Tillage	Organic matter (g kg^{-1})	Sand (%)	Silt (%)	Clay (%)	pH
Corn–corn	Chisel	25 (0.1) b	55	4	41	5.7 (0.2)
Corn–soy	Chisel	28 (0.1) b	21	59	20	5.9 (0.2)
Corn–forage–forage	Chisel	26 (0.2) b	29	43	28	5.6 (0.1)
Corn–corn	No-till	35 (0.3) a	33	28	39	5.7 (0.3)
Corn–soy	No-till	29 (0.2) b	35	25	40	5.8 (0.1)
Corn–forage–forage	No-till	37 (0.3) a	28	25	47	6.0 (0.1)

Lower-case letters represent significant differences at p < 0.05.

TABLE 2 | Mean and (SE) ($n = 3$) of biomass and nitrogen content for total aboveground production and fine root production sampled at harvest (October 2020) from a long-term trial comparing tillage and crop rotational diversity in Northwest Ohio.

Rotation	Tillage	Aboveground biomass (kg ha^{-1})	Aboveground *N* (kg N ha^{-1})	Fine root biomass (kg ha^{-1})	Fine root *N* (kg N ha^{-1})
Corn–corn	Chisel	16,669 (2,291)	300.2 (63.9)	3,774 (1,187)	32.8 (11.8) b
Corn–soy	Chisel	17,122 (1,543)	314.9 (34.4)	5,319 (1,212)	33.1 (6.5) b
Corn–forage–forage	Chisel	16,960 (2,979)	335 (101.2)	6,972 (1,672)	30.3 (0.4) b
Corn–corn	No-till	19,118 (752)	395.9 (20.1)	8,296 (810)	56.2 (5.3) a
Corn–soy	No-till	14,509 (1,818)	272.8 (33.7)	7,068 (3,011)	27.3 (4.7) b
Corn–forage–forage	No-till	15,968 (2,067)	341.4 (36.9)	6,269 (762)	69.1 (1.9) a

Means separation reflected by different lower-case letters represents significant differences at p < 0.05.

using lsmeans and significant difference was determined at $a = 0.05$. Treatment was treated as a fixed factors and block was treated as a random factor. For soil protein, NAG, EI, b1, and f2 a repeated measure randomized complete block design ANOVA was conducted using PROC MIXED procedure SAS v.9., with time being the repeated measure variable. Repeated measures was used to account for the variance within each sampling time point. Graphing was performed with ggplot2 in R (Wickham, 2016). Correlations were conducted using the Pearson's method cor.test function R 3.1.1 (R Development Core Team, 2020).

RESULTS

Organic Matter, Soil Texture, and pH

Rotation and tillage had a significant effect on organic matter ($p < 0.05$). The CC NT and CFF NT systems had significantly greater organic matter than all other systems (**Table 1**). Soil texture was similar between systems, however, NT systems and CC CT systems appeared to have greater clay content (%) than CS CT and CFF CT systems (**Table 1**). Lastly, pH was not significantly different between systems (**Table 1**).

Quantification of Plant and Soil Nitrogen Pools

Belowground N cycling varied between systems of contrasting tillage intensity and crop rotational diversity. For instance, tillage and crop rotation both had a significant main effect and there was also a significant tillage by crop rotation effect on FRN ($p < 0.05$). However, tillage was found to have the largest impact on FRN ($F = 11.85$; **Supplementary Table 2**). For instance, the CC NT and CFF NT systems had significantly greater FRN compared to all other systems (**Table 2**). Differences in tillage intensity and crop rotational diversity did not significantly impact FRB (**Table 2**). However, all NT systems and the CFF CT system FRB values trended higher. Aboveground plant compartments, including ABN and ABB were greatest in the CC NT systems, however, there were no significant effects for aboveground plant material (**Table 2**).

Soil N cycling was also significantly influenced by tillage intensity and crop rotational diversity. Tillage, rotation, and time were found to have significant main effects on soil protein ($p < 0.05$). In addition, tillage and rotation had a significant interaction effect on soil protein, however, tillage ($F = 21.1$) and rotation ($F = 21.09$) main effects were found to have the greatest impact on soil protein ($p < 0.05$), relative to the interaction effect between rotation and tillage (**Supplementary Table 3**). When averaged across all rotations, soil protein was 61% greater in the NT systems relative to the CT systems (**Figure 1**). The CC NT and CFF NT systems had significantly greater soil protein at harvest relative to all other systems and sampling time points (**Figure 1**). During planting all CS systems and CC CT systems were found to have reduced soil protein. In harvest, all CT systems and CS NT systems had reduced soil protein when compared to all other systems. Between planting and harvest soil protein increased in CC NT and CFF NT systems.

Rotation and time both had significant main effects on NAG activity ($p < 0.05$). In addition, tillage and time had a significant interaction effect on NAG activity ($p < 0.05$).

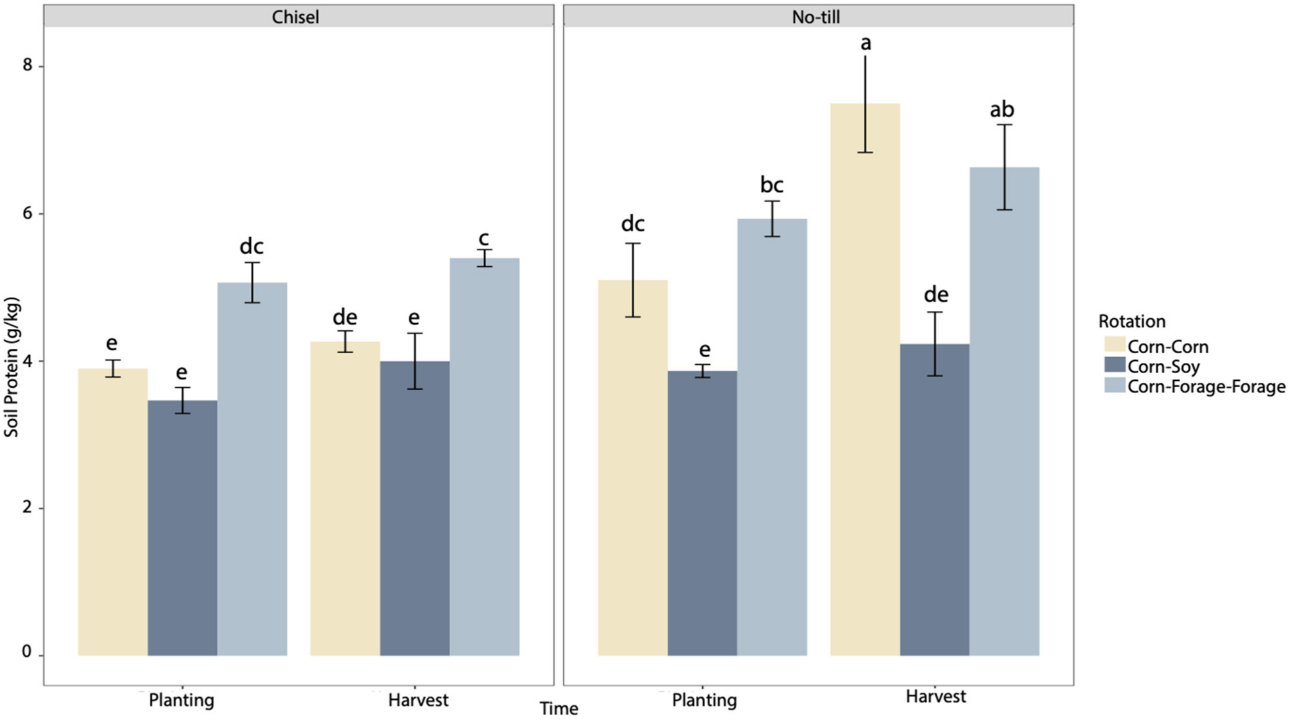

FIGURE 1 | Soil protein (g kg^{-1}) of three different crop rotations (corn–corn, corn–soy, corn–forage–forage) under no-till and chisel till treatments during two sample time points: planting (May 2020) and harvest (October 2020) (*n* = 3). Error bars represent one standard error of the mean. Means separation reflected by lower-case letters represent significant differences at $p < 0.05$ across all systems and time points.

However, rotation was found to have the greatest impact on NAG activity, when compared to all other factors ($F = 8.09$) (**Supplementary Table 2**). NAG enzyme activity was greatest in CFF CT systems during planting relative to all other systems in both planting and harvest (**Figure 2**). During planting CC NT systems had significantly reduced NAG activity. In addition, at harvest, CS crop rotations appeared to be significantly reduced in NT and CT systems. When comparing dynamics over the course of the growing season, NAG activity was found to decrease over time in all systems except that of CC NT, where NAG activity had elevated values at harvest.

Rotation had a significant effect on $b1$ enrichment opportunists ($F = 4.65$, $p < 0.05$; **Supplementary Table 2**). Nematode enrichment opportunists ($b1$) were found to be significantly greater in CS CT systems during planting when compared to CC planting, CS NT planting, CC CT harvest, and CFF CT harvest systems (**Table 3**). Although time did not have a significant effect, the abundance of $b1$ enrichment opportunists were found to decrease over time in CT treatments, and increase over time in NT systems. Fungal nematode enrichment opportunists ($f2$) and the EI were not significantly impacted by tillage or rotation; however, CFF CT systems had the greatest $f2$ abundances and EI (**Table 3**). Additionally, f2 abundances and EI were found to remain consistent over time.

Correlations Between Nitrogen Pools and Crop Productivity Across All Systems

Correlations were conducted between all plant and soil N pool indicators at harvest (**Table 4**). Broadly, positive relationships were found between most plant and soil N pools. Aboveground N was found to be positively and significantly correlated to ABB (Corr = 0.92, $p < 0.05$). Additionally, ABN had moderate and positive correlations with soil protein (Corr = 0.37, $p > 0.05$) and FRN (Corr = 0.31, $p > 0.05$). Aboveground biomass was weakly correlated with all indicators but had more moderate relationships with FRB (Corr = 0.31, $p > 0.05$), and FRN (Corr = 0.2, $p > 0.05$). Fine root nitrogen was positively and significantly correlated to soil protein (Corr = 0.60, $p < 0.05$; **Figure 3A**). In addition, FRN had moderate correlations with NAG (Corr = 0.34, $p > 0.05$; **Figure 3B**), FRB (Corr = 0.24, $p > 0.05$), and $b1$ (Corr = 0.50, $p > 0.05$; **Figure 3D**). Fine root biomass had weak relationships with all soil N pools, except that of a moderate relationship with NAG (Corr = 0.32) and was marginally significant at $p < 0.1$ (**Figure 3C**). NAG activity was found to have a stronger relationship with soil protein but it was not statistically significant (Corr = 0.63, $p > 0.05$) and NAG had a moderate relationship with nematode EI (Corr = 0.33, $p > 0.05$). Bacterial and fungal nematode enrichment opportunists had weak relationships to all soil N pools.

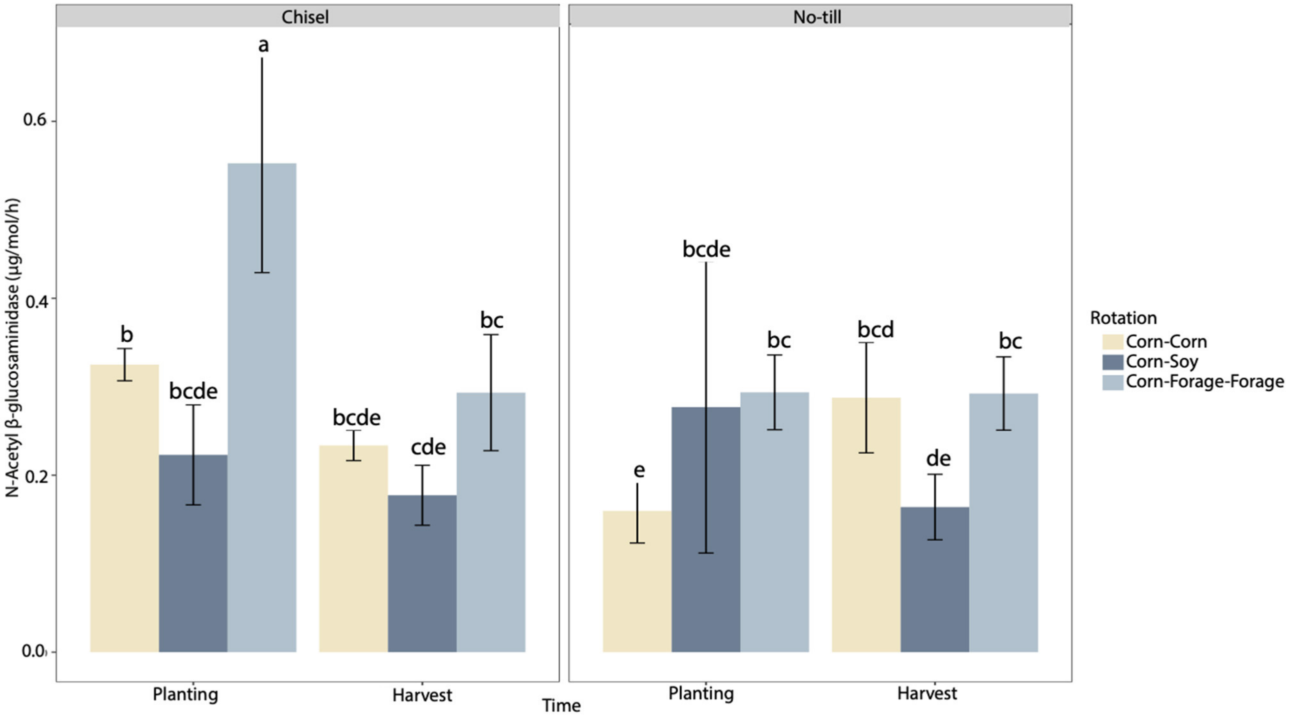

FIGURE 2 | N-Acetyl-B-Glucosaminidase (ug/mol/h) of three different crop rotations (corn–corn, corn–soy, corn–forage–forage) under no-till and chisel till treatments during two time points: planting (May 2020) and harvest (October 2020) ($n = 3$). Error bars represent one standard error of the mean. Means separation reflected by lower-case letters represent significant differences at $p < 0.05$ across all systems and time points.

TABLE 3 | Mean and (SE) ($n = 3$) of the abundance of enrichment opportunist bacterial feeders (*b*1), abundance of enrichment opportunist fungal feeders (*f*2), and the Enrichment Index (EI) from planting (May 2020) and harvest (October 2020) from a long-term trial comparing tillage and crop rotational diversity in Northwest Ohio.

Time	Rotation	Tillage	*b*1	*f*2	EI
Planting	Corn–corn	Chisel	4.3 (2.6) b	1.3 (1.9)	63.3 (32)
	Corn–soy	Chisel	37.0 (22.1) a	5.0 (5.0)	84.8 (7.7)
	Corn–forage–forage	Chisel	22.0 (12) ab	2.0 (2.0)	91.9 (4.1)
	Corn–corn	No-till	10.0 (6.1) b	0.0 (0.0)	64.4 (32)
	Corn–soy	No-till	1.0 (1.0) b	0.0 (0.0)	65.0 (33)
	Corn–forage–forage	No-till	27.7 (7.8) ab	5.0 (2.7)	90.3 (8.1)
Harvest	Corn–corn	Chisel	4.7 (4.2) b	0.3 (0.3)	81.2 (8.6)
	Corn–soy	Chisel	14.0 (10.0) ab	2.7 (1.8)	86.2 (5.8)
	Corn–forage–forage	Chisel	6.0 (5.0) b	6.7 (4.8)	76.6 (5.7)
	Corn–corn	No-till	11.7 (5.8) ab	0.0 (0.0)	76.8 (17)
	Corn–soy	No-till	26.3 (8.8) ab	2.1 (0.7)	36.2 (26)
	Corn–forage–forage	No-till	27.0 (15.0) ab	5.0 (3.2)	70.3 (11)

Means separation reflected by different lower-case letters represents significant differences at $p < 0.05$ across all systems and timepoints.

DISCUSSION

Here we used a long-term trial to examine how important organic N pools differ in systems that have been historically managed through the lens of conventional vs. ecological nutrient management. Specifically, we quantified plant and soil N pools in agroecosystems contrasting in crop rotational diversity and tillage intensity. In addition, this study aimed to investigate the relationship between N pools and crop productivity. Systems that incorporated perennial legumes and reduced tillage intensity enhanced belowground fine root N, N mineralization, and organic N pools. Crop productivity was also positively correlated with belowground N cycling, with fine root N being positively correlated to aboveground biomass.

Ecological Nutrient Management Enhances Belowground Plant Nitrogen Pools

We found that belowground N pools of FRN were greater under the no-till systems, where perennial legumes also played

TABLE 4 | Pearson's correlation coefficients (*r*) between plant and soil nitrogen pool indicators at harvest 2020.

	NAG	EI	FRB	ABB	FRN	ABN	b1	f2
Soil protein	0.63	0.08	0.22	0.20	0.60*	0.37	0.11	0.05
NAG		0.33	0.34†	0.16	0.34†	0.22	−0.03	0.02
Enrichment			−0.20	0.13	0.03	−0.02	−0.12	0.08
FRB				0.31	0.24	0.25	0.06	−0.20
ABB					0.23	0.92*	0.25	−0.31
FRN						0.31	0.50	0.15
ABN							0.20	−0.25
*b*1								0.33

†Significant at 0.10 probability level.
**Significant at 0.05 probability level.*

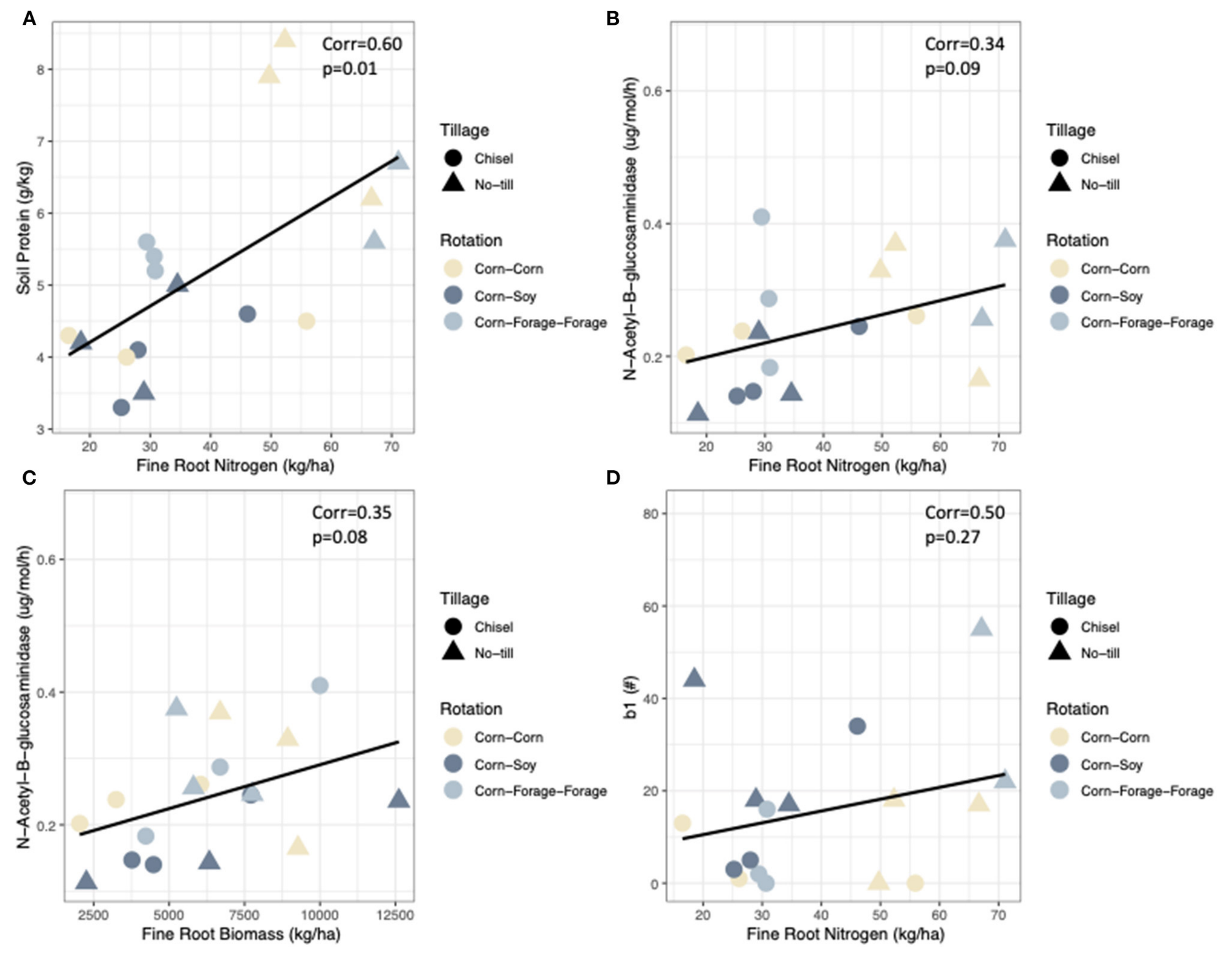

FIGURE 3 | Pearson's correlations between key nitrogen pools across contrasting agroecosystems **(A)** NAG (ug/mol/h) and FRB (kg ha^{-1}). **(B)** NAG (ug/mol/h) and FRN (kg ha^{-1}). **(C)** Soil protein (g kg^{-1}) and FRN (kg ha^{-1}). **(D)** Enrichment opportunists (*b*1) and FRN (kg ha^{-1}). The different systems are differentiated by shapes and colors, whereby shapes reflect tillage intensity and color represents crop rotational diversity.

a key role, identifying elevated levels under CFF relative to CS rotations. Leguminous perennials have greater fine root quality, and these nutrient deposits may have had an apparent legacy effect, through stimulating the quality of fine roots during the corn phase of the rotation (Frankenberger and Abdelmagid, 1985; Johnson et al., 2007; Tiemann et al., 2015). Generally, annual legume rotations in both intensities were found to have reduced FRN, which may have been due to the previous soybean crop depositing limited belowground biomass, thus reducing the amount of organic N deposited into the labile N pool and decreasing the N available for uptake in the corn crop rotation (Johnson et al., 2007; King et al., 2020). The elevated levels of FRN found within the NT systems, was most likely caused by decreased disturbance enhancing aggregate stability, which can result in greater organic N storage (McDaniel et al., 2014; King et al., 2020). Greater FRN indicates a faster turnover of fine roots, which primes the microbial pool and results in the rapid release of N into the soil system, thus alleviating N limitations (Gardner and Drinkwater, 2009; Dietzel et al., 2015; Tiemann et al., 2015; White et al., 2017; Jilling et al., 2018). Furthermore, the close proximity of fine roots to the soil can allow for greater N accrual through N deposits becoming enmeshed and protected in microaggregates (Rasse et al., 2005; Cates et al., 2016; Cates and Ruark, 2017). Although this study did not find differences among systems in aboveground plant N pools, belowground plant N pools are immensely important for long-term sustainability. For instance, Pugliese et al. (2019) found that belowground N deposited by perennial legume crops can be used toward plant re-growth. Specifically, greater FRN inputs can boost N organic pools and provide a greater amount of plant-available N during critical periods of corn growth, thus allowing for more efficient crop N uptake and yield (Culman et al., 2013; Osterholz et al., 2018; Pugliese et al., 2019). Our results therefore indicate that the use of a perennial legume in a crop rotation, rather than an annual legume, with reduced tillage intensity can enhance soil health through providing greater belowground organic N inputs.

Soil Nitrogen Pools Are Consistently Greater in Systems With Perennial Legumes

Soil N pools, which were measured through soil protein, NAG activity, and nematode enrichment opportunists were persistently greater in systems with perennial legumes, thus indicating improved soil health through organic N storage, and N mineralization. Labile pools of organic N within each system were measured using soil protein and were found to be greater in CC and CFF NT systems. This study also indicates that over the course of the growing season labile N pools increased in systems with the incorporation of a perennial legume. Similar to our findings other studies have also reported that the addition of a perennial legume in crop rotation systems may have also increased bulk N pools (Drinkwater et al., 1998; Jarecki and Lal, 2003; Grandy and Robertson, 2007; Carranca et al., 2015). The increases of soil protein within these systems may be caused by greater organic N inputs from perennial roots within the crop rotations (Cates et al., 2016; Sprunger et al., 2018). Enhanced labile N pools within systems with perennial legumes and less disturbance can increase soil quality, through increasing organic N storage and reducing N losses (Blesh, 2018, 2019). Specifically, perennial legumes have been shown to increase the amount of N in microaggregates (Tiemann et al., 2015). Moreover, labile N represents a pool that can also be easily accessed by soil organisms and made readily available to plants (Hurisso et al., 2018a). Thus, increasing the labile N pool also indicates a greater amount of organic N that can be utilized by subsequent crops (Blesh and Drinkwater, 2013). The increased organic N storage in systems of greater perenniality can also lead to reduced inorganic N additions (Bowles et al., 2020).

Systems where perennial legumes were incorporated also had greater N mineralization, which demonstrates the ability of these systems to provide greater N for crop uptake thus increasing crop productivity and soil health. Specifically, CFF rotations were found to have greater NAG enzyme activity, which represents the rate of microbial nutrient uptake and the chemical transformation of N (Tabatabai, 1994). In this study, the increase in NAG activity may be caused by perennial legumes within the crop rotation increasing substrate availability through enhanced N inputs (Geyer et al., 2016; Jilling et al., 2018). Additionally, our study indicated that CS rotations had reduced NAG enzyme activity, which may be caused by reduced biomass inputs from the previous soy crop, which decreased substrate availability for enzymes (McDaniel et al., 2014; Cates and Ruark, 2017). Our results indicated that the use of a perennial legume in annual crop rotations can augment N mineralization, which leads to improved soil health. That said, numerous other studies have found that lengthening rotations with annual legumes can also successfully enhance N pools and soil health (McDaniel et al., 2014; Tiemann et al., 2015; Perrone et al., 2020). The incorporation of legume cover crops has been shown to increase labile N pools relative to monocultures. For example, Liebman et al. (2018) found that hairy vetch (*Vicia villosa* var. AU Early Cover, HV) was successful at contributing the greatest levels of N into a corn based system relative to other cover crops, resulting in greater levels of inorganic N. Greater N pools in more diversified systems is likely due to the response of microbial communities leading to larger nutrient pools and enhanced soil quality (Bach and Hofmockel, 2015; Kallenbach et al., 2015). Enhanced enzyme activity in diverse systems has also been shown to positively affect aggregate formation and therefore lead to greater N retention (Tiemann et al., 2015; Austin et al., 2017).

In general, the nutrient enrichment opportunist values were highly variable and it was diffecult to detect an overall trend. That said, our results indicate that the CS system had a greater supply of N and enhanced nutrient enrichment than compared to CC at planting. Similarly, DuPont et al. (2009) also found greater *b*1 abundances in legume cover cropped systems compared to grain cover cropped systems. Monoculture systems lack diverse nutrient inputs, which may cause a decline in nutrient enrichment over time when compared to perennial and polyculture systems (DuPont et al., 2009, 2010; Tiemann et al., 2015; Song et al., 2016; Zhang et al., 2017b; Sprunger et al., 2019a; Wattenburger et al., 2019). More interesting is that both NAG and soil protein were found to be reduced in systems where *b*1 abundances were greater. This finding is parallel to Ugarte et al. (2013), which concluded that biologically based indicators may not be as effective as overall soil quality indicators. The incongruities between soil biological health indicators and overall soil quality indicators may be caused by the fact that soil biological indicators are more sensitive to changes in management and therefore reflect a more current state of soil function (Culman et al., 2013). These findings have important implications for plant growth, as bacterivore enrichment opportunists can accelerate the N mineralization rates and thus N availability for crop uptake (Yeates, 1999; Zhang et al., 2017b). Additionally, these results indicate that rotational systems that use a perennial or annual legume may result in greater N mineralization from soil fauna.

While enzymatic activity and soil protein were consistently greater in the CFF system, FRN and the enrichment of bacterial feeding nematodes were equivalent between CFF and CC systems. Despite these similarities, CFF systems are still more advantageous from an ecological nutrient management perspective relative to the CC systems. The perennial legumes are able to provide additional sources of N due to biological N fixation, and ultimately enhance N use efficiency within the crop rotation (Fujita et al., 1992). Roots of perennial legumes can allocate large amounts of organic N belowground, which can then be used for subsequent crop uptake from annual systems (Kavdir et al., 2005; Jungers et al., 2019). This additional source of N from perennial legumes can then reduce the amount of external inorganic N fertilizers needed to sustain subsequent corn crop yields (Yost et al., 2012; Blesh and Drinkwater, 2013).

Interactions Between Plant and Soil Nitrogen Pools Are Positively Related to Crop Productivity

This study found that plant–soil N pools, which were elevated in systems under ecological nutrient management, may result in enhanced crop productivity and soil health. Our correlation analysis revealed that ABN had positive relationships with soil protein, which indicates that enhanced soil quality is essential for greater crop productivity. These findings are supported by Glover et al. (2010) reporting that yields should be increased through enhanced soil quality rather than increased N fertilization. Moreover, this study indicates that ecologically managed systems can improve soil protein, thus indicating that these management strategies can also enhance crop productivity. We also found a positive relationships between FRN and soil protein, which indicates that FRN and soil protein may have a cyclical relationship in which the enhancement of both belowground plant and soil N pools can increase crop productivity. Furthermore, FRN was positively correlated with *b*1 abundances and NAG, representing a positive relationship between N mineralization and FRN. These positive relationships further reaffirm that the enhanced functioning of soil microbiomes is necessary for the cycling of nutrients and crop productivity (Griffiths, 1994; DuPont et al., 2009; Jansson and Hofmockel, 2020). Furthermore, these findings indicate that improving N cycling between plant and soil pools is essential for creating agricultural systems that can retain N and sustain yields (Sprunger et al., 2019b).

Ecological Nutrient Management Provides a Framework for Resilient Food Systems

Our study found that agricultural practices that fall within the ecological nutrient management framework such as increased crop diversity through the use of perennial legumes appear to play an important role in enhancing nutrient pools that bolster soil quality. This is especially important as improved soil quality is a key element within the United Nations Sustainability Goal 2.4, which seeks to implement agricultural practices that progressively improve land and soil quality (UN Sustainable Development Goals, 2020). While ecological nutrient management practices did not have a clear advantage in terms of crop production in this study, the increased organic nutrient pools found in the CFF systems could be important for prolonged food production and climate resiliency. In recent years, the Midwestern United States has experienced enhanced flooding due to extreme rainfall events, which has been shown to reduce the availability of inorganic N and substantially reduce crop yields (Alaoui-Sosse et al., 2005; Yin et al., 2020). Furthermore, increased perenniality within agroecosystems could provide more flexibility for farmers, where rotations could remain under forage crops. This could be especially important in regions where early summer flooding events prevent the planting of annual row-crops, as was evident across the Midwestern Corn Belt in 2019 (Lawal et al., 2021). That said, there are certainly food security trade-offs associated with leaving rotations under perennial forage, as increased acreage under forages reduces overall food production for human consumption (Reckling et al., 2016). For this reason, it will also be important to consider other types of perennial crops that could be produced for both grain and forage, including perennial intermediate wheat grass and perennial cereal rye (Ryan et al., 2018; Pugliese et al., 2019). Thus, perennializing agriculture could serve as an effective way toward meeting sustainable food production goals in the face of climate change. However, such alterations will take time as there are currently barriers to breeding, weed management, and market opportunities in perennial grain cropping systems (Ryan et al., 2018).

CONCLUSION

Ecological nutrient management strategies including the incorporation of perennial legumes into crop rotations and reduced tillage intensity present a solution for creating resilient agroecosystems because of their ability to enhance key rhizosphere processes. Our findings demonstrate that crop rotations that are lengthened with perennial legumes are capable of increasing belowground organic N inputs, N cycling through microbial communities and microfauna, and soil organic N storage. Moreover, perennial legumes in conjunction with no-till management have the capacity to increase soil health and sustain crop productivity. That said, continuous corn systems were also able to sustain certain soil N dynamics and fine root N levels when compared to corn rotated with perennial legumes. Despite these similarities, rotations that include perennial legumes are still more adventagous from an ecological nutrient management perspective as such rotations have more efficient N cycling and are less dependant on external fertilizer inputs. The positive relationships found between belowground plant N pools, and soil N pools demonstrates the need for agroecosystems that maximize belowground production, as rhizosphere processes are essential for improved soil health and building resilient agroecosystems. Perennial crops and legumes in conjunction with reduced tillage intensity should be considered when working to design agroecosystems that seek to meet United Nations Sustainability Goals related to food production and climate adaptation.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct and intellectual contribution to the work, and approved it for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.705577/full#supplementary-material

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Potential Contribution of Groundnut Residues to Soil N and the Influence of Farmer Management in Western Uganda

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Through symbiotic biological nitrogen fixation (BNF), grain legumes, such as groundnuts, can enhance soil nitrogen (N) and be an important source of N fertility, as well as a critical component of human nutrition and food security. Because legumes obtain N from soil N stocks as well as BNF, legume residues are key to capturing potential N benefits for soils, which may contribute to increased yields and food production. Here, we conducted a detailed survey at household and field level within a six-village corridor along the western boundary of Kibale National Park (KNP) in western Uganda. We focused on groundnut production and residue management practices and soil organic carbon (SOC) and total N (TN) in fields managed by 100 different households. We also determined SOC and TN in adjacent uncultivated KNP soils. We tested for relationships between socioeconomic factors and farmer groundnut management practices. We calculated a partial N balance and estimated potential N benefits under three scenarios for groundnut BNF. Within the study area, groundnut residue management varied greatly with 51% of surveyed farmers retaining residues on fields through spreading or incorporation, and 49% removing residues, either by transfer to banana groves or burning. Groundnut population density was relatively high with 43% of fields having >30 plants m^{-2}. Despite providing net N inputs of up to 27 kg N ha^{-1}, there was no observed effect of groundnut residue management practices on SOC, TN, or soil C:N ratios. Compared to uncultivated KNP soils, groundnut fields had lower mean levels of SOC and TN and wider C:N ratios. These values are consistent with cultivated soils; however, losses of SOC and TN were lower compared to losses previously reported for conversion from tropical forest to agricultural use. We found that farmer valuation and perception of groundnut residues were influential factors in residue management practices. Overall, we estimated that groundnut residues have the potential to contribute to SOC and TN stocks if retained in the field, but, conversely, removal will result in sizable losses. We find that both environmental and social contexts must be considered when recommending legumes for N provisioning services.

Keywords: nitrogen fixation, soil fertility, residue management, groundnut (*Arachis hypogaea*), smallholder farmers

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INTRODUCTION

Nutrient depletion is a primary factor in soil degradation and low and declining crop yields across sub-Saharan Africa (SSA) (Stoorvogel and Smaling, 1990; Tully et al., 2015a). Among countries in SSA, Uganda experiences some of the highest rates of land degradation, resulting in lower agricultural productivity (Stoorvogel and Smaling, 1990; Wortmann and Kaizzi, 1998; Nkonya et al., 2005). Compared to global averages, inorganic fertilizer use across SSA is very low at 16 kg ha arable land^{-1} year^{-1}, and it is extremely low in Uganda at 1.8 kg ha arable land^{-1} year^{-1} (World Bank, 2016). In Uganda, inorganic fertilizer accessibility, availability, and affordability is limited for smallholder farmers (Omamo, 2003). Organic inputs are often the main option for smallholder farmers and are a potentially more environmentally sustainable nutrient source. However, resource-limited farmers often find organic fertilizers, such as animal manure or compost, challenging to obtain or employ, especially at recommended amounts (Nandwa and Bekunda, 1998). Similarly, farmers face multiple pressures and trade-offs with crop residues, which in addition to being organic inputs, are frequently used as livestock feed and cooking fuel, among other purposes (Erenstein et al., 2015; Tittonell et al., 2015; Valbuena et al., 2015). Nationally, only 15% of Ugandan households reported adding organic or inorganic fertilizers or pesticides to common beans (*Phaseolus vulgaris* L.), and only 14% added these inputs to maize (*Zea mays* L.) (UBOS, 2013).

Nitrogen (N) is most often the main limiting nutrient for plant growth and crop yields (Sanchez et al., 1997). In natural ecosystems and low-input cropping systems such as those found across SSA, legumes can play a vital role in N provisioning. Legumes access N from the atmosphere *via* biological N fixation (BNF) to support growth and the production of high protein grains and N-rich residues (Snapp et al., 1998; Giller, 2001). Legume residues can supply immediate and short-term N to subsequent crops, as well as contribute to long-term N and soil fertility by stimulating microbial biomass production, nutrient cycling and maintenance of or gains in soil organic matter (SOM) (McDonagh et al., 1993; Toomsan et al., 1995; Promsakha Na Sakonnakhon et al., 2005; Srichantawong et al., 2005; Franke et al., 2018; Kermah et al., 2018). Legumes are therefore widely recommended as an organic N source for low-input, resource-limited agroecosystems in SSA where they can supply N critical to both healthy soil functioning and crop production and potentially replenish SOM in degraded soils (Snapp et al., 1998, 2018; Giller, 2001). Importantly, legumes are also critical for human health, nutrition, and dietary diversity as a key source of protein, diverse amino acids, micronutrients, dietary fiber, and phytochemicals (Messina, 1999; Foyer et al., 2016). Indeed, poorer households in SSA rely on legumes for a large proportion of their dietary protein (Akibode and Maredia, 2012) and because of their importance, legumes can often be sold for high prices at local and international markets, generating substantial income for resource-poor households (Snapp et al., 2018). Because of their many potential benefits, legumes are recommended as part of ecological nutrient management and conservation agriculture schemes in SSA with the ultimate goal of improving soil health, and thus the sustainability and resiliency of low-input agroecosystems (Thierfelder et al., 2013; Drinkwater et al., 2017).

Across SSA, farmers grow grain legumes for provision of food and income, in addition to BNF benefits. The two most widely grown grain legumes in SSA and in Uganda are common bean and groundnut (*Arachis hypogaea* L.) (UBOS, 2014; Snapp et al., 2018). Because common bean often has low rates of BNF, supplying limited amounts of N in rotation with cereals, we chose to focus on groundnuts. Groundnuts are capable of fixing substantial amounts of N and have a moderate-to-low harvest index, and so can supply a relatively high quantity of N in rotation with cereals (Giller et al., 1997; Ojiem et al., 2014; Franke et al., 2018). Despite N-rich grain removal with harvest, grain legumes with a relatively low harvest index can deliver substantial N benefits to soil; groundnut residues have been found to provide up to 139 kg N ha^{-1} (Ojiem et al., 2014). However, N credits or gains from legumes are notoriously challenging to determine in the field (Cadisch et al., 2000; Unkovich and Pate, 2000). Fixation efficiency and total quantity of N fixed can vary dramatically depending on legume variety, agroecological conditions (e.g., site, climate, weather, soil type, and fertility), and management practices (e.g., cropping patterns, fertilization) (Peoples and Craswell, 1992; Wani et al., 1995; Dakora and Keya, 1997; Mokgehle et al., 2014). Because legume N fixation is highly variable across cultivar, agroecology, and management, legume N credits are almost always an estimation of potential legume N contributions. In order to fully understand the potential for legume N credits on smallholder farms, we need more long-term data and site and context specific information, including farmer residue management practices, which are key to maximizing both N and C contributions of legume residues to soil (Wani et al., 1995; Giller et al., 1997; Kermah et al., 2018).

Within these agroecosystem contexts, including soil fertility, climate, and management practices, nutrient balances that calculate the N inputs and outputs of a farming system can serve to estimate or quantify legume N benefits (Tully et al., 2015b). Nutrient balances help to highlight the advantages and/or disadvantages of inputs, outputs, and/or management practices in terms of economic, agricultural, and ecological sustainability (Nkonya et al., 2005; Haileslassie et al., 2007). In conjunction with nutrient balances, examination of the relationships among household demographic/socioeconomic characteristics and management practices can elucidate the factors driving farmer decision-making and further contextualize and assess the sustainability of agroecosystems (Nkonya et al., 2005; Ebanyat et al., 2010a). Socioeconomic and demographic factors such as gender of the household head or crop planner (Nijuki et al., 2008; Tanellari et al., 2014; Mugisa et al., 2015), land tenure (Place and Otsuka, 2002; Kassie et al., 2015), ethnic group (Naughton-Treves, 1997; Kirner, 2010), and field distance from the homestead (Tittonell et al., 2005, 2013; Zingore et al., 2007a) have been shown to drive farmer practices and affect farmer access to, use, and decisions regarding resources like residues (Barrett and Bevis, 2015).

Few studies have examined the potential N benefit from grain legumes in SSA while simultaneously adjusting and accounting for legume crop management practices and different fates of legume residues. We present a case study of farm management and residue practices with a focus on groundnuts within smallholder agroecosystems in western Uganda. We collected soils, GIS, socioeconomic and management data and estimated three levels of potential N addition *via* groundnut BNF. Our objectives were: (1) to assess differences in groundnut residue management; (2) to estimate the potential N benefit from groundnut residues based on their management; (3) to determine if groundnut residue management impacts SOC and TN; and (4) to explore soil and socioeconomic factors driving groundnut residue management practices. We hypothesized that groundnut residue retention in fields had the potential to deliver positive N balances at the field-scale. We expected TN to be greater and soil C:N to be narrower in fields in which groundnut residues were consistently retained vs. fields in which groundnut residues were continually removed. Lastly, we predicted that socioeconomic factors previously identified in the literature as drivers of farmer practices would also be linked to groundnut residue management practices.

MATERIALS AND METHODS

Study Area

Research was conducted along the western border of Kibale National Park (KNP) in Burahya County, Kabarole district, western Uganda (**Figure 1**). KNP and the surrounding area fall within the Albertine Rift, a biodiversity hotspot that is part of Africa's Rift Valley (Lepp and Holland, 2006). KNP received its national park designation in 1993, but it has existed as a forest preserve since 1932 (Struhsaker, 1997). The park is a remnant of transitional forest isolated within a densely populated agricultural landscape; in 2006, the population density within 5 km of the park boundary was estimated to be ∼300 individuals km^{-2} (Hartter and Southworth, 2009). Outside KNP, the hilly landscape is dominated by small-scale agriculture, tea plantations, grassland, and fuelwood plantations (Chapman and Lambert, 2000; Majaliwa et al., 2010). Smallholder farms adjacent to the park are impacted by crop raiding by park animals and subsequent crop losses are fairly common, though it mainly impacts those within 1 km of the boundary (Hartter, 2010). The main regional cash crops are banana (*Musa* spp.), tea (*Camellia sinensis* L.), coffee (*Coffea arabica* and *Coffea canephora*), and maize, but smallholder farmers grow over 20 species of subsistence crops (Hartter and Southworth, 2009). Kabarole district is characterized as an area of "high agricultural potential" (de Jager et al., 2004), and ∼84% of households engage in crop growing or livestock agriculture (UBOS, 2014). The district had the highest maize production in the western region (UBOS, 2010). Kabarole district lies within the Lake Albert Crescent zone, which has good to moderate soils (FAO, 2010). Related to the high population density, the western region has the smallest average landholdings at 0.8 ha compared to the national average of 1.1 ha (UBOS, 2010). The small landholdings and high population density are driven in part by limited land (Hartter and Southworth, 2009).

The study area covered the villages of Kanyawara, Kyakabuzi, Isunga, Iruhuura, Nyabweya, and Kajumiro, which fall along an ∼22-km north-south transect along the edge of the KNP's western boundary (**Figure 1**). The study area is located between latitude 0.57–0.39°N and longitude 30.35–30.32°E and lies along an elevational gradient north to south from 1,550 to 1,100 m above sea level. The climate is tropical with an average daily temperature range of 15–23°C (Struhsaker, 1997). Rainfall in the region is bimodal with two rainy seasons separated by two dry seasons. The first dry season from early December to late February is followed by a rainy season occurring from approximately early March through mid-to-late May. A second dry season extends until early September followed by a rainy season from September through November (Hartter et al., 2012). Planting commences at the start of each rainy season, allowing for two growing seasons each year. Mean annual rainfall ranges from 1,100 to 1,700 mm with rainfall decreasing and temperature increasing when moving from north to south along the elevational gradient (Struhsaker, 1997). Soils are classified as eutrophic volcanic ash and ferralitic sandy clay loams. Study area soils were previously established to be inherently medium to highly fertile (Jameson, 1970).

Surveys and Data Collection

We conducted a survey and soil sampling within the six village areas in July 2015, coinciding with the final growing stage and harvest of groundnuts and maize (July harvest for groundnut and July to early August harvest for maize) planted at the start of the first rainy season (March–April planting for groundnut and February–March for maize). The study comprised 100 households that had actively been growing groundnuts (Kanyawara $n = 9$, Kyakabuzi $n = 9$, Isunga $n = 21$, Iruhuura $n = 18$, Nyabweya $n = 16$, Kajumiro $n = 27$). All households were located within ∼1.6 km from the closest park boundary. Ugandan field assistants translated survey questions and responses from English into Rutooro and Rukiga, the respective languages of the resident Batooro and Bakiga ethnic groups. Households within each village were approached at random and asked if they grew groundnuts and were willing to participate in a survey. A two-part survey instrument was used: (1) a household socioeconomic and overall farm survey, which collected information on family size and composition, education level, ownership status and size of agricultural fields, livestock ownership, crop planting and harvesting dates, crop yields, crop use, income received for specific crops, perceived causes for declines in crop yields, land management decisions, and resource concerns; and (2) a survey of farmer management for the farmer-identified primary groundnut field, which provided information on any and all inputs and outputs into that field, field preparation, any steps taken or practices used to increase or maintain soil fertility, the field's cropping history for the two previous seasons (September 2014–February 2015 and March–August 2014), and detailed information on all crops grown in the field that season (March–August 2015), including planting and harvesting dates and methods, yields, or expected yields for that season, crop use (household, saved, or sale), and detailed residue management with reasons for specific practices. The residue management practices described by respondents were categorized into four main practices: (1) "remove" included

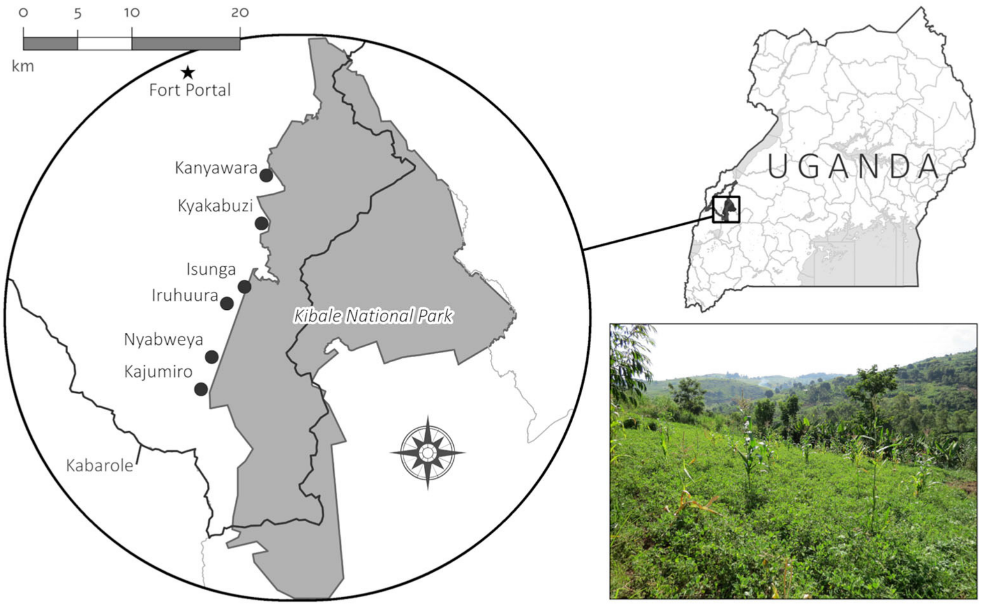

FIGURE 1 | Map of study area, with a focus on areas surrounding six villages along the western border of Kibale National Park in Kabarole district, western Uganda. The inset photo shows a surveyed field in which groundnut is planted as a ground cover with maize sparsely interplanted within a hilly terrain, representative of the majority of fields surveyed for this study.

residues removed from the field and transported to another location, (2) "burn" included residues burned within the field, (3) "spread" comprised residues that were kept on the field as mulch and spread on the field surface, and (4) "incorporate" constituted residues that were retained and buried into the soil. A simple relative wealth ranking of the study area farms was constructed by assigning a value to assets of homestead dwelling construction and livestock ownership ("yes" and "no" responses to whether they owned cattle, pigs, goats, chickens, other; Hockett and Richardson, 2018); values were summed and then categorized into "below average," "average," and "above average" based on the interquartile range.

The first part of the survey instrument (the household and whole farm survey) had previously been implemented with 14 households in July 2013 and eight households in June 2014. We used these prior responses in our analysis. In July 2015, these households participated in the second part of the survey instrument, the field survey.

The survey was administered at the homestead and at the field. The homestead and the corresponding field were marked as waypoints on a handheld Garmin GPS 62s unit. Respondents or a capable household member walked us around or clearly indicated the perimeter of the groundnut field, which was saved as a track to the GPS unit. The GPS data was retrieved from each unit and read into ArcGIS 10.4 software. A map of the household locations, field locations, and field perimeter tracks was created using ArcGIS. We calculated the area within the perimeter track to determine the size of each surveyed field and determined the Euclidean distance between the homestead and groundnut field. Fields within 50 m of the homestead were categorized as "homefields," and fields further than 50 m were categorized as "outfields" (Zingore et al., 2007b).

Within each surveyed field, we used quadrats and total plant counts to measure plant density for groundnut and any other crop present. In each field, we measured the groundnut crop by counting the number of individual plants within four 50 × 50 cm quadrats; the location of each of the four quadrats was randomly determined along a diagonal field transect. The large variation in the density of crops interplanted in a groundnut field necessitated different measurement techniques according to intercrop species and/or field size. Intercrop plant density was measured either by counting plants within four 50 × 50 cm quadrats (beans) or three 3 × 3 m quadrats (all other crops except banana and coffee) or by counting the total number of plants in the field (coffee, banana, or intercrops in fields smaller than ∼0.03 ha). If groundnut or an intercrop had already been fully harvested, we asked respondents to provide an estimate of the crop density by indicating the plant layout within a quadrat.

Soil Sampling and Analysis

In each groundnut field, three soil samples were taken at random to a depth of 15 cm using a 2-inch diameter soil probe and composited to represent each field. We used a set of KNP reference soils ($n = 12$) collected from uncultivated forest areas (Tiemann, unpublished data) proximal to each village in the study area as a baseline comparison to groundnut field SOC and N values. All fields were within 4 km of the proximal reference soils, and in prior exploratory analyses there were no significant differences in texture between field and park soils. It is likely soils were from the same parent material, and oxalate extractions of these soils show no significant differences in the iron and aluminum oxides between field and proximal park soils (Tiemann, unpublished data). Soils were air-dried in Uganda and shipped to Michigan State University (MSU) in East Lansing, MI, USA, for analysis.

Soil samples were passed through a 2 mm mesh sieve and 5 g placed into 20 ml scintillation vials to oven-dry at 60°C for 24 h. Oven-dried soils were ground on a roller mill and subsamples weighing ∼20 mg were packed into tins to measure SOC and TN on an elemental analyzer (ECS 4010, Costech Analytical Technologies, Inc., Valencia, CA, USA).

Partial N Balance

To construct partial N balances, we first used the literature to determine a harvest index for groundnut of 0.23 (Phoomthaisong et al., 2003; Ncube et al., 2007; Kermah et al., 2018). Using the farmer reported yields and field size calculated from the collected GPS data, we calculated total groundnut aboveground productivity (ANPP, kg biomass ha^{-1}). Next, we subtracted the harvested grain amount (grain, kg groundnuts ha^{-1}) from the total biomass and converted this remaining aboveground residue biomass to biomass N (stover N, kg N ha^{-1}) assuming groundnut residues contain 2% N (Kanmegne et al., 2006; Ncube et al., 2007). Assuming a grain N content of 3.8% N (Kanmegne et al., 2006; Ncube et al., 2007) we converted total grain yield to grain N (grain N, kg ha^{-1}). We summed the stover N and grain N to determine the total crop N (crop N, kg N ha^{-1}).

Because the proportion of N derived from BNF can be highly variable, we conducted a sensitivity analysis whereby we adjusted the proportion of total plant N from fixation, or what we term the BNF efficiency, to 30, 50, and 70%. In other words, we assumed 70, 50, or 30% of total plant N was mined from the soil rather than obtained *via* BNF. These proportions of N derived *via* BNF fall within the range of published groundnut N and fixation values for SSA (Kanmegne et al., 2006; Ncube et al., 2007; Ojiem et al., 2007; Ebanyat et al., 2010b; Nyemba and Dakora, 2010; Mokgehle et al., 2014; Franke et al., 2018; Kermah et al., 2018; Oteng-Frimpong and Dakora, 2018). We multiplied the crop N by the proportion of N derived *via* BNF to find the fixed N (fixed N, kg N ha^{-1}). Our final calculations then accounted for farmer reported management of stover (proportion stover retained %). When farmers reported removing or burning all groundnut residue, we estimated that residues would provide 5% (incomplete burning or removal) of their total potential N benefit to soils, or if farmers provided an estimated percentage of residues remaining, this value was used instead. For groundnut residues that were reported incorporated into the soil or spread on the field surface, we estimated that 100% of the potential N benefit could be delivered. We calculated N mined from soil as:

$$N_{soil}\ (\text{kg ha}^{-1}) = \text{crop N} - \text{fixed N} \tag{1}$$

Finally, the partial N balance is the difference between N mined from soil and removed in grain harvest vs. retained in stover as based on management and calculated as:

$$\begin{aligned}\text{Season N balance (kg N ha}^{-1}\text{ season}^{-1}) &= \\ \text{stover N} * \text{proportion stover retained (\%)} &- N_{soil}\end{aligned} \tag{2}$$

Additionally, to explore the total amount of N potentially conferred by a groundnut crop we calculated a second partial N balance assuming that 30% of fixed N was present belowground (Unkovich et al., 2008). Including the 30% fixed N contribution from roots (fixed N/0.70; Kermah et al., 2018), the total N mined from soil was calculated as:

$$\text{Total } N_{soil}\ (\text{kg ha}^{-1}) = \text{crop N} - \text{fixed N}/0.7 \tag{3}$$

And the season N balance plus belowground contributions (Total season N balance, kg N ha^{-1} $season^{-1}$) as:

$$\begin{aligned}\text{Total season N balance (kg N ha}^{-1}\text{season}^{-1}) &= \\ \text{stover N} * \text{proportion stover retained (\%)} &- \text{Total } N_{soil}\end{aligned} \tag{4}$$

We calculated the partial, single season, field-level N balance for 77 groundnut fields; out of the 100 fields, 12 were missing field area measurements because of an error with the handheld GPS, four were missing groundnut plant density measurements, and seven fields were excluded because the reported groundnut yield weights were extreme outliers (>3,000 kg ha^{-1}, more than 1.5 times interquartile range).

Data Analysis

Descriptive statistics, Pearson's chi-square tests, Wilcoxon rank-sum test, and analysis of variance (ANOVA) were performed with STATA/IC 14.2 statistical software (StataCorp, College Station, TX).

Pearson's chi-square test of independence was used to measure the strength of relationships between the four residue management practices and socioeconomic factors, including ethnicity, village, gender of the household head, crop planner, land tenure, wealth ranking, distance from the field to the homestead, and factors related to a household's valuation of groundnut. The factors related to valuation of groundnut were derived from three different survey questions asking: "which crop do you sell the most of?;" "which crop do you make the most profit on?," and "which crop is the best to plant if you want to improve crop yields/soil fertility?" Because data were not normally distributed, we applied the Wilcoxon rank sum test to test for differences between groundnut field soils and KNP reference soils (Corder and Foreman, 2009).

Groundnut field SOC and TN values were normalized by calculating the difference from proximal KNP baseline soils. We performed a one-way analysis of variance (ANOVA) on the normalized C and N values by groundnut residue management practice.

RESULTS

Household and Farm-Level Characteristics

Household demographic and socioeconomic characteristics are presented in **Table 1**. Households ranged in size from 1 to 20 people with a mean of 6.3 members ($sd = 3.30$), with 61% of members under the age of 15. Most respondents identified as belonging to the Bakiga ethnic group (72%) and 25% identified as Batooro. Households were predominately designated as male-headed (74%). Despite this, 44% identified a woman as the crop planner, i.e., the person responsible for planning the planting and harvesting schedule (29% of male-headed households had a female crop planner), 26% identified a man, and 29% identified multiple planners.

Land ownership was high with 75% of households owning all their land and 24% of households renting a portion of their land. Mean, farmer-estimated, household land use was 3.3 ha. The majority (57%) of households had similar, average wealth, while 24% were below average and 19% were above average. The above average wealth ranking includes households that owned cattle (12%) in addition to other livestock and had a dwelling constructed of concrete (10%); average households owned goats, pigs, and/or chickens and had homes with mud-wattle construction and an iron-sheet roof; and below average households owned chickens or no livestock and had traditional thatch-roofed homes or homes with dirt floors.

TABLE 1 | Demographic and socioeconomic characteristics of the 100 surveyed groundnut-growing households along the western edge of Kibale National Park in western Uganda.

Variable		%
Land Tenure, own all land		75
Ethnicity of respondent		
	Batooro	25
	Bakiga	72
	Other[a]	3
Household head gender		
	Female	25
	Male	74
Crop planner		
	Woman	44
	Man	26
	Multiple	29
Wealth ranking[b]		
	Below average	24
	Average	57
	Above average	19
Household livestock holdings		
	Cattle	12
	Pigs	60
	Goats	73
	Chickens	82
	None	8
Intercrop maize with groundnut		68
Rotate maize with groundnut		54
Groundnut most sold crop		22
Groundnut most profitable		34
Groundnut best for soil fertility		57
"Very much" dependent on crop sales		77

[a] Other includes Bakonjo, Iteso, and Munyankole.

[b] Wealth ranking is based on the assignation of numerical values to housing materials and livestock assets. The assets were summed to create a continuous variable representative of wealth (Hockett and Richardson, 2018).

In addition to groundnuts, households grew a large diversity of crops at the farm-level with, in order of frequency, maize, common bean, banana, cassava, potato, and sweet potato grown by over half the households (**Table 2**). Crop production at the farm-level was strongly characterized by intercropping (99%) and crop rotation (82%). Maize was often intercropped with groundnut (68%), and of the 70% of farms that reported practicing a set, planned crop rotation, 77% reported that they included groundnut in the rotation. The top three reasons for intercropping were limited land (45%), greater harvest (22%), and greater profit (16%). When asked which crop(s) were best to plant for improving soil fertility, 57% included groundnut, though 30% of respondents also listed at least one non-legume crop (sorghum, maize, potato, millet, rice, and bananas were also mentioned).

Maize was reported as the most sold crop (48%) with groundnut the second most sold crop (22% of households). Groundnut was reported to be the most profitable crop in 34% of households, followed closely by maize (31%), then rice (14%) and potato (10%). Most households (77%) categorized themselves as "very much" dependent on income from crop sales.

The large majority of farmers (93%) reported seeing year-to-year declines in crop yields with declines most often reported in maize (68%), followed by groundnut (48%), common bean (46%), and potato (27%); 6% of farmers reported declines in all crops. The reasons cited for declining crop yields included factors relating to soil fertility (soil fertility loss, old soils, poor soils, 43%), climate (heavy rains, drought, delayed rains, climate change, 34%), crop management (poor seeds, crop type, delayed planting, 5%), and a combination of soil, crop, and climate factors (11%); 7% said they did not know the reason.

Groundnut Field Characteristics: Production and Use

Groundnut fields ranged from 0.01 up to 0.58 ha with a mean area of 0.095 ha (**Table 3**). The distance between the surveyed groundnut fields and the homestead was at minimum 5 m and maximum of 1.7 km. The distance was <50 m for 40% of households thereby characterized as homefields and >50 m for 60%, which were classified as outfields.

All fields were rainfed and were prepared and worked manually with a hand hoe. Only 14 fields had received any kind of external input; seven fields had manure added, four had herbicide applications, and application of chemical fertilizer, household waste, or residues from another source occurred in single fields. The remaining 86 fields did not receive any external inputs other than seeds or starts at planting. Weed biomass was retained on

TABLE 2 | Frequency of each crop grown at the household level with normal seasonal yields and the frequency of each crop grown in the groundnut field surveyed during the 2015 study season (crops other than groundnut indicate intercrops) and for the two prior growing seasons.

	Farm-level		**Groundnut field crop frequency**			
Crops	**Farm production frequency**	**Mean yield[a]**	**Study season[b]**	**Previous season**	**Two seasons prior**	**Residues removed[c]**
	%	**kg farm^{-1} season^{-1}**	**%**	**%**	**%**	**%**
Groundnut	100	189	100	3	7	49
Maize	100	963	73	46	44	57
Common bean	96	134	2	31	31	58
Cassava	92		54	7	3	41
Banana	89	314 bunches	11	3	2	0
Potato	82	499	4	16	7	0
Sweet Potato	75	374	0	5	12	40
Millet	41		0	7	8	13
Rice	37	490	0	20	10	20
Soyabean	15		2	2	0	50
Sorghum	14		2	1	2	40
Pea	14		4	5	1	40
Coffee	12		6	2	1	0
Taro	10		6	0	0	50
Tomato	7		0	1	1	0
Onion	6		0	1	1	50
Fruits[d]	5		0	0	0	na
Other[e]	10		6	2	1	11

[a] *Farm level yield data collected for select crops; values reported per farm, total farm area not measured.*
[b] *Study growing season March–Aug 2015, previous season Sept 2014–Feb 2015, two seasons prior March–Aug 2014.*
[c] *Percentage of fields from which over half the residues were consistently removed or burned over the span of three seasons.*
[d] *Fruits include avocado, jackfruit, mango, guava, pineapple.*
[e] *Tea, cabbage, pumpkin, sugarcane, hot pepper, eggplant, eucalyptus.*

96% of fields, and 93% of fields were weeded 1–2 times per season with the remainder weeded more frequently.

Of the three seasons surveyed, all fields were planted to groundnut during the 2015 survey season, but only 10% of households reported planting groundnut in the surveyed fields during the two prior seasons. This is contextualized by the fact that groundnut was included every third season in 83% of reported rotations. Approximately 52% of households grew maize and 50% grew common bean at least once during the two prior seasons. In 66% of surveyed fields, farmers reported using crop rotations with a variety of crops, including groundnut (79%), common bean (74%), maize (56%), potato (56%), rice (36%), cassava (21%), and sweet potato (21%; **Table 2**). Crop combinations, densities and rotations in these groundnut fields were highly variable. We found anywhere from one to five different intercrops planted with groundnuts in a variety of combinations, the most common of which was groundnut-maize-cassava in 21% of fields. On average, farmers had planted groundnut in the surveyed field for $\sim$4 seasons total out of seven years in crop production.

For the surveyed groundnut field, household consumption accounted for around half of the groundnut harvest (48%), while 26% of the harvestwas sold and 25% was saved for seed. All households except for one intended a portion of the groundnut yield for household use, 80% of households saved part of the harvest for seed and 58% sold a portion of the groundnut harvest.

Bunch-type groundnut was found in all fields with varieties identified as local. The mean planting density for groundnut was 29 plants m^{-2} (**Table 3**), with 43% of households planting 30 or more groundnut plants m^{-2}. In all surveyed fields, groundnut was planted as a ground cover over the entire field. Maize and cassava were interplanted at much lower densities and widely dispersed with respective mean planting densities of 0.44 (SEM = 0.62) and 0.18 (SEM = 0.04) m^{-2}. Planting density for the other less common intercrops (**Table 2**) was also low, ranging from <0.01 to 0.63 plants m^{-2} with a mean of 0.136 m^{-2} (*SEM* = 0.03). Regression of groundnut yield on groundnut planting density indicated no linear relationship ($R^2 = 0.015$) between the two; the exclusion of outliers did not increase the R^2 above 0.1.

All farmers harvested groundnuts by pulling the entire plant out of the ground. Of the 100 groundnut-producing households, 49% removed or burned groundnut residues and 51% retained groundnut residues on fields, either incorporating or spreading the stover as a mulch (**Table 2**). Groundnut residues were removed from 19% of fields, burned in 30%, spread on the surface for 31%, and incorporated into the soil in 20%. Residues from maize, the most common intercrop, were removed to mulch bananas in 46% of fields, surface spread in 32%, incorporated in 11%, and burned in 11%. Approximately 41% of cassava residues were removed to use as firewood or animal feed, and 59% of residues were replanted as stem cuttings or remained in the fields.

TABLE 3 | Groundnut field characteristics and agronomic data across 100 smallholder farms along the western edge of Kibale National Park in western Uganda.

Variables	*n*	Mean	Minimum	Maximum	SEM
Field Size (ha)	88	0.095	0.01	0.58	0.01
Distance from homestead (m)	100	199	5	1,658	29
Groundnut planting density (m^{-2})	96	29	5	60	1.07
Maize planting density (m^{-2})	68	0.44	0.004	1.44	0.05
Groundnut yield (kg ha^{-1})	88	1,143	47	4,752	114
Groundnut yield designated for:					
Household use (%)	99	48	0	100	0.03
Saved seed (%)	99	25	0	100	0.02
Sale (%)	99	26	0	88	0.03
Maize yield (kg ha^{-1})	66	751	9	3,581	101
Maize yield designated for:					
Household use (%)	68	85	0	100	0.04
Saved seed (%)	68	4	0	100	0.02
Sale (%)	68	12	0	75	0.03

Respondents provided a variety of reasons and explanations for residue management practices for groundnut and other crops planted in the field over the course of the three seasons (**Figure 2**). However, of all the different crop residues, only groundnut residues were described as having potentially negative impacts on the soil or crop yields (**Figure 2**). A total of 18 respondents said they burned or removed groundnut residues because the residues were either bad for the soil or caused infertility. Conversely, residues were described as adding fertility by 26 respondents who spread, incorporated, or removed residues to use as mulch in other fields. Residue decomposition was mentioned often with 10 respondents stating that they burned or removed groundnut residues because they did not easily decompose, whereas 11 respondents said they spread or incorporated residues so they would decompose.

Soil Fertility

Study area soils are high in organic matter with relatively high SOC and TN values and low C:N (**Table 4**). In comparison to uncultivated reference soils from KNP that represent total potential soil nutrient stocks, the cultivated groundnut field soils contained 24% less total SOC, 44% less TN, and had a 35% wider C:N ratio. In two of the villages, Kyakabuzi and Isunga, mean SOC values were higher than proximal KNP reference soils, but TN values were lower and C:N ratios wider. An analysis of variance on the normalized groundnut field SOC and TN values found that groundnut residue practices did not significantly alter SOC ($P = 0.695$) or TN ($P = 0.742$) (**Figure 3**).

Groundnut Field N Balance

The partial N balance scenarios showed there were N benefits at 50 and 70% BNF efficiency but only if residues were retained, i.e., spread or incorporated, in which case, mean BNF efficiency benefits ranged from ∼8 up to 27 kg N ha^{-1} (**Figure 4**). Removal and burning of groundnut residues resulted in N loss at all levels of BNF efficiency with the greatest losses of 76 and 60 kg N ha^{-1}, respectively, at 30% BNF efficiency (**Figure 4**). Although belowground biomass estimates for groundnut are not well-characterized, using values reported in the literature, and assuming 30% N fixed was allocated to belowground productivity, at the highest level of BNF efficiency (70%) root N could balance N lost through residue removal (**Supplementary Figure 1**).

Determinants of Groundnut Residue Management

Household socioeconomic characteristics were not strongly related to groundnut residue management practices, but variables related to valuation of groundnut were. Pearson's chi-square measures of association did not find significant relationships between groundnut residue management and the ethnicity of respondent, gender of the household head, crop planner, land tenure, wealth ranking, distance from the field to the homestead, or if groundnut was the most sold crop (**Table 5**). There was a significant relationship between the removal of groundnut residues and village with more respondents than expected removing residues in Kanyawara, and fewer than expected in the remaining villages, except for Isunga ($P < 0.05$).

Households that considered groundnut as one of the best crops for improving soil fertility were significantly associated with residue incorporation and residue spread ($P < 0.05$) (**Table 5**). Households that designated groundnut as the most profitable crop were significantly associated with burning (**Table 5**). Finally, farmers who perceived groundnut residues as "bad" for soil or crop fertility were significantly associated with burning ($P < 0.0001$) and were not associated with spreading ($P < 0.01$) or incorporating residues ($P < 0.05$).

DISCUSSION

In this study we took an agroecological approach, integrating biophysical, social, and economic data, to determine the extent and drivers of SOC and TN relative to groundnut management within smallholder farm fields in western Uganda. We documented the smallholder household, farm and groundnut field characteristics in the western region, an agroecosystem that is not well-profiled in the literature. We found that SOC and especially TN have been depleted relative to uncultivated soils. Despite groundnut appearing to be the most promising source of N for these fields, contrary to our hypothesis there were no discernible significant differences by groundnut residue management practice on SOC, TN, or C:N. It appears that groundnut residues have not had a large impact on soil C and N, which could be due to: residue application methods (timing, location, quantity, etc.); limited impact of aboveground residues compared to belowground contributions throughout the season; cropping system heterogeneity, including a complex variety of intercropped and rotated crops and planting densities. Estimated partial N balances supported our hypothesis that groundnut residues could deliver positive N balances at the field-scale. Residues could make up for grain N losses and deliver considerable N in these low

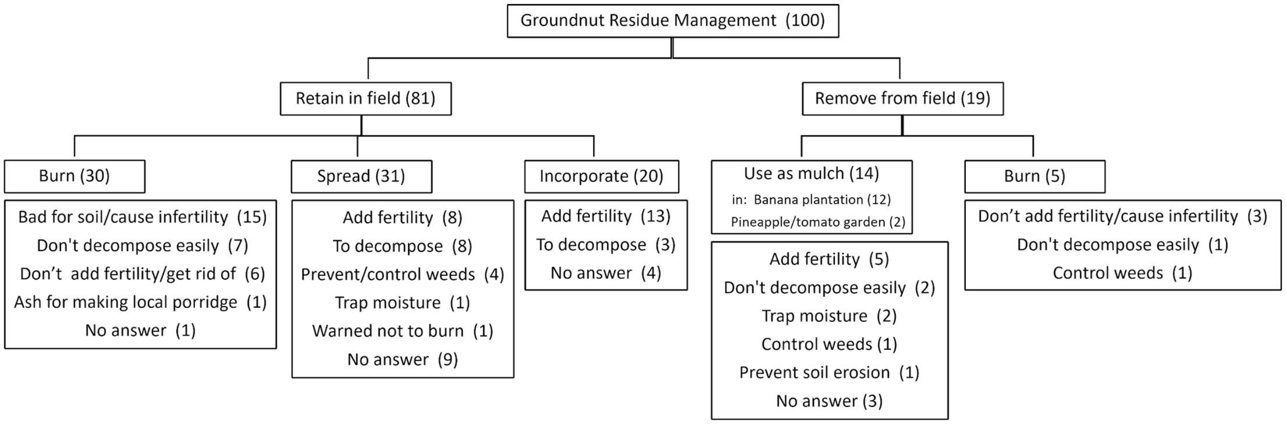

FIGURE 2 | Tree diagram illustrating potential fates of groundnut residues on smallholder farms in Kabarole district, western Uganda, with farmer provided explanations for each of the five practices. Number of farmer responses for each management practice or explanation are in parentheses.

TABLE 4 | SOC, TN, and soil C:N ratios in soils collected from groundnut fields and corresponding, proximal reference soils from Kibale National Park (KNP).

Groundnut field soils by village				**KNP reference soils**		
	C	**N**	**C:N**	**C**	**N**	**C:N**
	g kg^{-1}	**g kg^{-1}**		**g kg^{-1}**	**g kg^{-1}**	
Kanyawara	43.62 (6.48)	3.11 (0.42)	13.89 (0.87)	87.28 (30.04)	7.78 (1.90)	10.70 (1.09)
Kyakabuzi	62.67 (5.53)	4.46 (0.36)	13.95 (0.25)	52.79 (8.87)	5.66 (0.63)	9.21 (0.51)
Isunga	52.19 (2.38)	3.24 (0.16)	16.25 (0.57)	52.61 (2.84)	3.69 (0.25)	14.32 (0.52)
Iruhuura	54.12 (2.77)	3.38 (0.18)	16.11 (0.32)	52.61 (2.84)	3.69 (0.25)	14.32 (0.52)
Nyabweya	42.35 (1.67)	2.89 (0.10)	14.65 (0.23)	48.77 (3.46)	4.15 (0.25)	11.75 (0.41)
Kajumiro	33.22 (2.22)	2.16 (0.13)	15.25 (0.27)	48.77 (3.46)	4.15 (0.25)	11.75 (0.41)
Mean	46.03 (1.52) a	3.02 (0.10) a	15.27 (0.17) a	60.36 (8.22) b	5.32 (0.65) b	11.50 (0.63) b

Isunga and Iruhuura share a reference soil, as do Nyabweya and Kajumiro. Values are means followed by one standard error of the mean (SEM; in parentheses) and letters, where different, indicate significant differences between groundnut cultivated soil compared to KNP soils.

P-values for comparison of KNP to groundnut fields: SOC $P = 0.044$; TN $P = 0.000$; C:N $P = 0.000$.

input fields at close to 70% BNF. Importantly, only half of surveyed farmers retained groundnut stover in their fields, and removal or burning of residues resulted in N losses at all levels of BNF. Residue management practices were not clearly linked to socioeconomic factors related to gender and wealth, but rather highly driven by perception and valuation of groundnut residues as either good or bad for soil fertility or crop yields. We identify important knowledge gaps with respect to groundnut management, residue management and SOM or N benefits from legumes in SSA, as well as the importance of including information about residue management and variety selection to maximize BNF efficiency when legumes are recommended as a component of ecological nutrient management.

Current Soil Fertility

On average, the cultivated groundnut field soils are degraded compared to the uncultivated KNP reference soils. However, the mean difference in SOC (24%) is less than the reported C decline in other studies comparing tropical forest soils to cultivated fields (Tiessen et al., 1994; Moebius-Clune et al., 2011). Time of conversion from forest to field is unknown and likely variable for these fields as pockets of remnant forest outside the park boundary were cleared for agriculture over a broad time frame. However, it is likely that most fields were cleared by the 1970s when large waves of migrants settled in the region (Ryan and Hartter, 2012). A global meta-analysis examining SOC stocks after land use change found that conversion from native forest to crop resulted in a decline of ∼50% in the top 30 cm (Guo and Gifford, 2002). A chronosequence in a region of Kenya with similar bimodal precipitation found that the degree of soil degradation in cultivated fields vs. primary forest was highly influenced by soil parent material (Moebius-Clune et al., 2011). The andic soils in our study area have relatively young overlays or rift volcanics that exhibit inherently high levels of fertility, renewed through mineral weathering, and characterized by amorphous mineral colloids with large active surfaces to which organic matter readily binds (Young, 1976). The soils have low bulk density, high water holding capacity, and good drainage, making them optimal

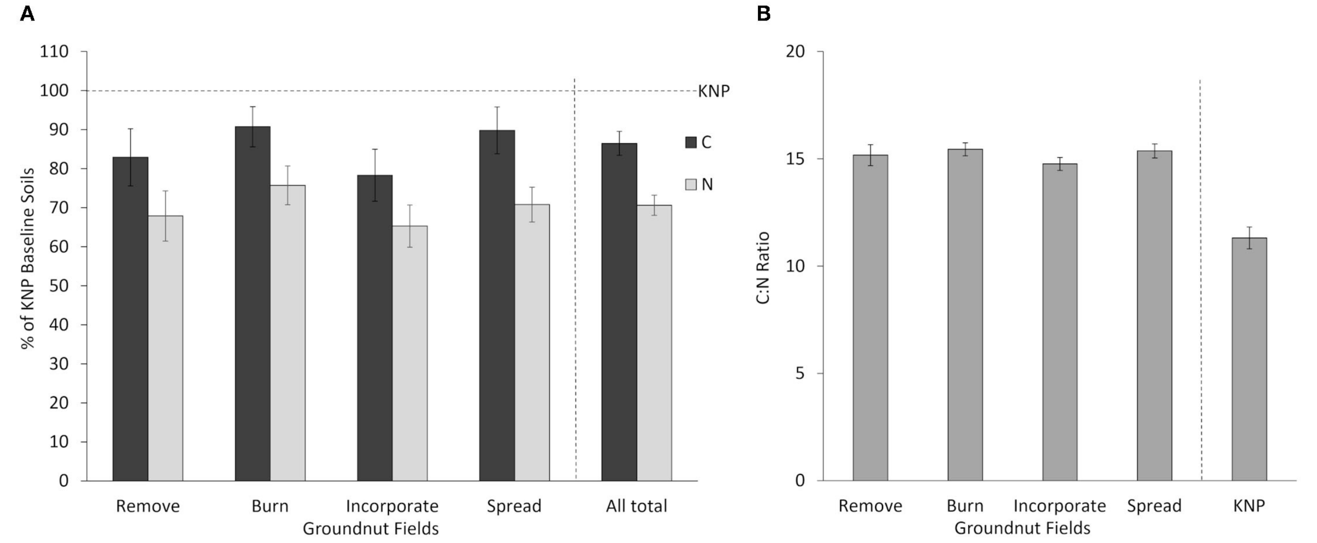

FIGURE 3 | Mean groundnut field ($n = 100$) SOC and TN as a percentage of uncultivated Kibale National Park (KNP) reference soils ($n = 12$) **(A)** and groundnut field soil C:N ratios compared to the C:N ratio of KNP soils **(B)**. Across all groundnut fields, SOC ($P = 0.044$) and TN ($P = 0.000$) were significantly reduced compared to KNP soils. By residue management practice, there were no significant differences between KNP and groundnut fields in SOC, TN or soil C:N ratios. Data are means ± one standard error.

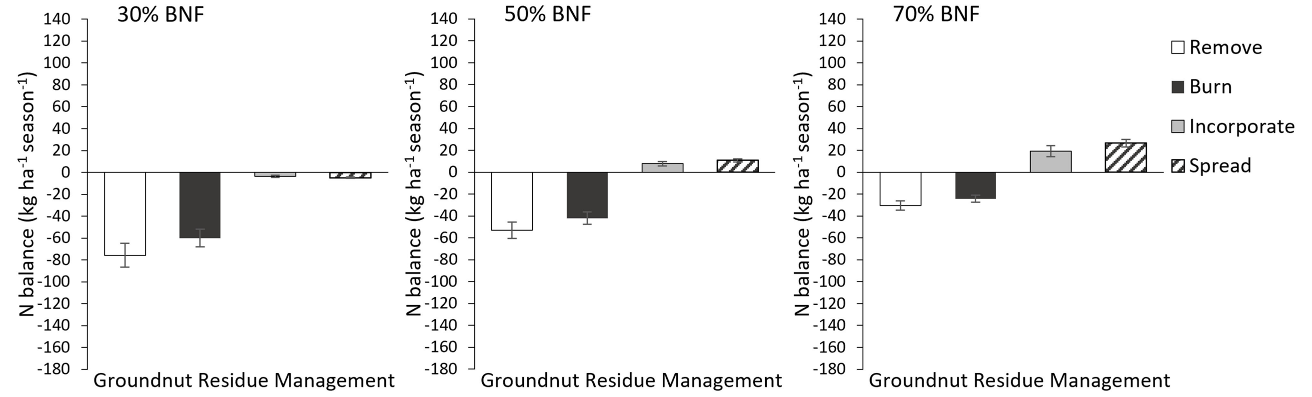

FIGURE 4 | Potential single-season N balances for groundnut fields ($n = 77$) surveyed in 2015 in Kabarole district, western Uganda. N balances account for N removal through grain harvest calculated at three BNF efficiencies, i.e., percentage groundnut plant N from BNF relative to total plant N demands, and grouped by residue management practice. Data are means ± one standard error.

for plant growth (Shoji et al., 1993). These properties have likely buffered the soils against degradation and C loss in the surveyed fields.

Farmer field management may also have contributed to maintaining or even recouping SOC lost due to forest conversion as farmers intercrop and/or rotate a large diversity of crops (**Table 2**). According to a review of SOC change after adoption of different management practices in tropical croplands, the strongest predictors of C change were quantity of C inputs, experiment duration, and management practices; soil, and climate variables did not have an effect (Fujisaki et al., 2018). The review determined that the management practice that resulted in the highest SOC was diversified crop rotation. In the current study, farmers practiced diversified crop rotation, but high rates of crop residue removal (**Table 2**) diminished the quantity of organic matter inputs. Removal of groundnut stover, relatively high in N content, not only removes important organic matter from the system but also a prime N source. The wider C:N ratio found in groundnut fields compared to uncultivated KNP soils is indicative of high N demands that are not being met by organic matter inputs. Instead, competition for N would tend to be high, which may result in microbial N mining of extant SOM (Craine et al., 2007). The addition of high-quality groundnut residues could provide N and help to narrow the C:N ratio of SOM in farmer fields.

TABLE 5 | Relationships between demographic and socioeconomic characteristics, farmer preferences, and groundnut residue management practices in smallholder farm fields along the western border of Kibale National Park ($n = 100$).

			Percent respondents			
		n **100**	**Remove (*n* = 19)**	**Burn (*n* = 30)**	**Incorporate (*n* = 20)**	**Spread (*n* = 31)**
Ethnicity	Batooro	25	24	24	12	40
	Bakiga	72	17	32	24	28
	Other	3	33	33	0	33
	P-value		0.59	0.75	0.31	0.52
Village	Iruhuura	18	6	39	22	33
	Isunga	21	29	33	14	24
	Kajumiro	27	15	26	33	26
	Kanyawara	9	56	11	0	33
	Kyakabuzi	9	11	22	22	44
	Nyabweya	16	13	38	13	38
	P-value		0.03*	0.67	0.28	0.85
Household head gender	Female	25	20	28	28	24
	Male	74	19	31	18	32
	P-value		0.88	0.77	0.47	0.24
Crop planner	Woman	44	14	39	20	27
	Man	26	31	15	12	42
	Multiple	29	17	31	28	24
	P-value		0.33	0.43	0.48	0.20
Land tenure, own all land	Yes	75	20	31	16	33
	No	24	17	29	33	21
	P-value		0.83	0.80	0.16	0.17
Wealth ranking	Below average	24	17	29	13	42
	Average	57	16	28	25	32
	Above average	19	32	37	16	16
	P-value		0.3	0.77	0.41	0.19
Distance from homestead	Homefields	40	15	30	23	33
	Outfields	60	22	30	18	30
	P-value		0.41	1.00	0.61	0.79
Groundnut most sold	Yes	22	18	36	14	32
	No	78	19	28	22	31
	P-value		0.91	0.46	0.40	0.93
Groundnut most profitable	Yes	34	15	47	15	24
	No	66	21	21	23	35
	P-value		0.43	0.01*	0.34	0.25
Groundnut best for soil fertility	Yes	57	21	28	28	23
	No	43	16	33	9	42
	P-value		0.55	0.63	0.02*	0.04*
Groundnut residue “bad” for fertility	Yes	18	17	83	0	0
	No	82	20	18	24	38
	P-value		0.78	0.00***	0.02*	0.00**

Data from surveys conducted in July 2015.

*Significant at $P < 0.05$.

**Significant at $P < 0.01$.

***Significant at $P < 0.001$.

Impact of Groundnuts on SOC and TN

The potential N contribution from groundnut stover if efficiently recycled to soil could increase N availability and thus boost yields and biomass of following crops, creating a positive cycle for C and N additions to the soil (**Figure 4**). However, we did not detect evidence of positive benefits of groundnut residue retention to SOM (**Figure 3**). SOC, TN, and C:N ratios did not differ significantly from uncultivated KNP soils across groundnut fields based on groundnut residue management practices. While these results are somewhat surprising, there are several potential explanations. First, higher biomass and yields of other intercrops or rotated crops with subsequent removal of their residues may reduce or cancel out potential benefits of groundnuts to the soil. For example, we found that 57% of farmers consistently removed maize residues, either through removal to the banana plantation as mulch or through burning (**Table 2**). For other commonly planted crops like common bean, cassava, and sweet potato, residue removal was also high at 58, 40, and 37%, respectively (**Table 2**). Without residual biomass retention from maize, common bean, and other crops within these fields, potential for SOM gains from groundnut stover are severely limited.

Second, groundnut residues alone may not be enough to influence SOM and TN, though they may positively impact crop fertility. The N inputs from groundnut would be expected to be relatively short-lived in the soil with residue N being mineralized and then immobilized by microbes and/or taken up by plants. The N provided by groundnut residue has the potential to stimulate productivity of intercropped or rotated crops such that residue inputs are increased with positive impacts on SOM and TN. Approximately 43% of farmers reported rotating groundnut every third season (i.e., every other year, similar to legume-maize rotations in tropical systems with unimodal precipitation) on the surveyed groundnut field. However, in this case, the N inputs from groundnut stover retention vs. non-retention were possibly not great enough, frequent enough, or available at the necessary time or place to significantly impact productivity and residue inputs from other crops.

Finally, the lack of a detectable effect of retention vs. removal of groundnut residues is also surprising given that in the study area, groundnut was planted at a density higher than the official recommendation by Uganda's National Agricultural Research Organization (NARO) of 15 plants m^{-2} for unirrigated production and closer to the recommended 30 plants m^{-2} for irrigated fields (Okello et al., 2013). Also, all farmers planted groundnut over the whole field rather than the recommended spacing of 30–45 cm rows (Okello et al., 2013); broad field coverage has many possible advantages including reduced soil erosion and weed competition. "Square spacing," or the equal spacing of groundnut plants over the growing area, has been shown to have positive benefits and to maximize both total plant biomass and groundnut yield (Jaaffar and Gardner, 1988; Gardner and Auma, 1989). Results in the literature are mixed regarding groundnut plant population density and its effect on grain yield and stover production, groundnut variety, and growth habit (bunch vs. runner). Environmental conditions are critical to the density at which yields and biomass are maximized; maximum density values ranged from 20 to 50 plants m^{-2} (Bell et al., 1987; Bell and Wright, 1998; Tarimo and Blarney, 1999). Aboveground biomass has been shown to increase with increasing plant density, while pod yield has been shown to be less responsive and to decline at densities >25 plants m^{-2} (Bell et al., 1987; Tarimo and Blarney, 1999). Documentation of on-farm (vs. researcher-managed) groundnut planting density and spacing is scant in the literature (e.g., Nyemba and Dakora, 2010), and our study documents relatively high plant densities with yields equivalent to on-farm trial yields in similar agroecological zones in western Kenya where somewhat lower planting densities were employed (Ojiem et al., 2007). If the high planting density equated to a large volume of aboveground biomass with correspondingly moderate-to-low grain yield as suggested by previous studies (Bell et al., 1987; Tarimo and Blarney, 1999), the potential net C and N input should be sizable, yet we saw no evidence of this potential benefit in SOC and TN.

Groundnut Residue Management Practices

If aboveground residues are retained on fields, farmers can maximize the full N benefits from groundnut BNF but, in the current study, we found that 49% of farmers did not retain groundnut residues, although almost two thirds of farmers were using residues as some sort of soil amendment across their farm (**Figure 2**). The assumption that legumes like groundnuts can improve soil fertility, increase crop yields, and produce high-protein, more nutrient dense crops is largely based on best management practices. Studies that specifically address smallholder farmer management of groundnut residues are rare in the literature, and the existing research often does not represent smallholder contexts well. Several studies in Thailand present what may be considered an optimal potential N credit from groundnut residues as the groundnut crop was seeded, fertilized, and managed according to recommended best practices (McDonagh et al., 1993; Toomsan et al., 1995, 2000; Phoomthaisong et al., 2003; Srichantawong et al., 2005). In these studies, groundnut residues were chopped to 10 cm lengths, which would greatly impact rates of decomposition and timing of N availability to a subsequent crop, and is a labor-intensive step that the majority of smallholder farmers are unlikely to take (McDonagh et al., 1993; Toomsan et al., 1995, 2000; Phoomthaisong et al., 2003; Srichantawong et al., 2005). While groundnut residues retained on fields could contribute N to a following crop, another potential hurdle is the timing of N release from residues, and the N demand by a following crop is difficult to predict and synchronize (Robertson et al., 1997). Two studies that looked at the time gap between the planting of the next crop and the post-harvest surface-application or incorporation of groundnut residues found no significant differences in N delivery from surface-applied vs. incorporated residues, although trends suggested higher residue N conservation in soil and efficiency of N recycling, as well as slightly higher yields, with incorporation (Promsakha Na Sakonnakhon et al., 2005; Srichantawong et al., 2005). One study also tested removing and storing the groundnut residues before incorporating them just prior to maize planting and found that this significantly boosted maize yield compared to immediate post-harvest residue incorporation, surface application, and removal; however, the authors concluded that the storage facility and labor requirements made this practice difficult for smallholder farmers to implement (Promsakha Na Sakonnakhon et al., 2005). These studies emphasize the value of keeping residues in the system irrespective of application method. Overall, there is a lack of studies on groundnut residue contributions to soil N and none seem to fully replicate resource-limited, smallholder farmer management practices.

Factors Driving Groundnut Residue Management Practices

In the study area, groundnut residue management practices appear to be driven by perceptions and valuation of groundnut stover. Respondents gave various explanations for groundnut residue management decisions, and these decisions seem to be largely based on the perception of groundnut residue fertility or utility, and human values and behaviors that are part of the social context (**Figure 2**). Most farmers explained that they incorporated or spread groundnut residues in the field or as mulch in the banana plantation because residues added fertility. Bananas are the main staple food crop, and the transfer of residues to the banana plantation to boost yields through the benefits of added fertility, trapped soil moisture or weed prevention, makes sense in these resource-limited agroecosystems. On the contrary, most farmers who burned residues in the field, or removed residues and burned them elsewhere, perceived groundnut residues as "bad" for the soil, causing soil infertility or not benefiting soil fertility (**Figure 2**). Respondents were often not able to explain their reason for believing groundnut stover was "bad," but several farmers mentioned burning had been recommended in the past as means to eradicate disease and/or pests (e.g., rats), which are noted concerns with residue retention (Erenstein, 2002). The basis for the negative perception of groundnut residue within the study area warrants further investigation.

We found no strong relationships between groundnut residue management practices and social and economic factors that have previously been shown in the literature to be drivers of farmer management decisions in SSA (e.g., gender of the household head, crop planner, ethnic group, land ownership, wealth rank, field distance from the homestead). Perhaps, in this region of Uganda, these socioeconomic drivers are less important than those related to farmer perception of groundnut fertility or there are other factors related to farmer resources that are more important determinants of residue management practices (**Table 5**). A commonly identified tradeoff in the literature is the use of residues as livestock feed (Tittonell et al., 2015; Valbuena et al., 2015), but livestock holdings are low in the study area and no household indicated that groundnut residues were used to feed livestock; only sweet potato and cassava residues were distinguished as animal feed. Respondents who listed groundnut as their most profitable crop were more likely to burn the residues, which is a relationship that requires further exploration as it could be linked to various different drivers, such as time and labor availability, residue biomass amount, and management at farm-scale.

In order to make effective recommendations and to enhance adoption of beneficial practices it is important for any extension or agricultural development agency working within the region to know and understand drivers of management practice. This knowledge is necessary for devising and implementing local or regional policy, for example residue burning regulations.

Groundnut Residue Management Impacts on Soil N Balance

The groundnut field N balances were calculated using estimated N input from groundnut residues minus the N exported by groundnut grain while also factoring in residue management practices (i.e., spreading, incorporating, removing, or burning). The N input from fully-retained, i.e., incorporated or spread, groundnut residues could provide a substantial N credit at 70% BNF (**Figure 4**). The maximum N benefit from groundnut residues at 70% BNF is ∼27 kg N ha^{-1} $season^{-1}$, which is considerable in a no-to-low-input system. Giller and Cadisch (1995) estimated that to offset N losses in SSA, a legume crop needed to fix an average of 30 kg N ha^{-1} $year^{-1}$, and with retained residues and belowground inputs groundnut could likely achieve this at close to 70% BNF efficiency (**Supplementary Figure 1**). However, there are a number of factors that combine to determine the N provisioning potential of groundnut stover, most of which have been inadequately researched, including: stover quantities and N concentrations under different climates and soil types; roots and rhizodeposition; BNF efficiencies across varieties and environmental conditions and intercrop arrangements; and management of residues (e.g., timing of addition, spreading vs. burying, etc.).

We performed a sensitivity analysis to examine a span of BNF efficiencies, not only to reflect the fact that BNF can fluctuate by variety and season-to-season (Mokgehle et al., 2014; Oteng-Frimpong and Dakora, 2019), but also because there is no precedent for groundnut BNF on soils with such high TN, where legume nodulation and BNF may be suppressed by large pools of available soil N (Giller and Cadisch, 1995). Studies in SSA have contrasting conclusions about the impact of soil N on BNF efficiencies, for example, one determined that high endogenous levels of soil N led to lower N fixation (Mokgehle et al., 2014), while another found that BNF was lower in low fertility vs. high fertility fields and BNF generally decreased with soil fertility levels (Ojiem et al., 2007). Intercropping legumes with cereals and other non-N fixing crops, as was the case in 88% of the groundnut fields we surveyed, can lead to reductions in soil N concentrations that then promote greater nodulation and BNF (Giller and Cadisch, 1995), but only if BNF is not limited by other nutrients.

Residue management is also critical to achieving an N benefit and if groundnut stover were removed, groundnut would be a heavy miner of soil N at <70% BNF efficiency (**Figure 4**). Even our simplified N balances confirm the importance of management in combination with BNF as field balances were only positive when residues were spread and incorporated (**Figure 4**). We chose to use the maximum of 100% N delivery for residues that were spread or incorporated to help illustrate the full potential N benefit of groundnut stover. If there was loss of retained residue (e.g., through livestock grazing or pests) or loss of retained residue N (e.g., through ammonia volatilization, denitrification, or nitrate leaching), which is likely, then nutrient balances would be reduced (**Figure 4**). Further, we chose to use a minimum of 5% N delivery for residues that were burned or removed, though it is probable that the total combustion of residues is inconsistent, as is the proportion of residue material left in the field. Importantly, the field-scale partial N balance establishes reference points for farmers, extension agents, and policymakers when estimating a *potential* N credit from groundnut residues within the context of management practices.

While the partial N balances do not account for the N loss from the diverse number of additional crops grown at the field-scale and other potential inputs and outputs, the estimated N inputs suggest that full retention of residues at the higher levels of BNF could reduce or counter additional N exports over a full cropping cycle. The average seasonal maize yield for western Uganda is ∼2,600 kg ha^{-1} $season^{-1}$ (UBOS, 2010), which would remove about 41 kg N ha^{-1} $season^{-1}$ at a maize grain N concentration of 1.57% (Kaizzi et al., 2012). This output could be balanced by groundnut N inputs if BNF efficiency was close to or >70% and residues were retained (**Figure 4**; **Supplementary Figure 1**). Notably, when a second set of N balances were calculated considering the belowground N inputs from unrecovered roots and nodules and rhizodeposition contributions, which have been estimated to account for 30 to 50% of plant N (Giller et al., 1997; Unkovich and Pate, 2000; Herridge et al., 2008), we see that there is potential for even greater N input from groundnut (**Supplementary Figure 1**). Additionally, there could be N contributions from the other legume crops grown on these farms (i.e., common bean and pea), but relative to groundnut their N contributions are likely far less as common bean has been shown to be poor at BNF and pea is not widely grown (Herridge et al., 2008; Franke et al., 2018).

With fields planted to groundnut receiving the only substantial N inputs (through BNF), our results suggest that overall N balances at the farm-level would be negative considering the mean yields and diversity of other crops, and the lack of other N inputs (fertilizer or manure) to these crops (**Table 2**). Negative farm-level N balances would be in line with previously published nutrient balances in Uganda which found negative or near zero N, P, and K values at all levels of scale across all regions of the country, with few exceptions (Stoorvogel and Smaling, 1990; Wortmann and Kaizzi, 1998; Briggs and Twomlow, 2002; Bekunda and Manzi, 2003; de Jager et al., 2004; Sheldrick and Lingard, 2004; Nkonya et al., 2005; Ebanyat et al., 2010a; Mubiru et al., 2011; Lederer et al., 2015). More positive farm-level N balances might be achieved through an increase in groundnut production, or inclusion of non-harvested legumes such as those in cover crops or agroforestry species.

Increasing groundnut grown through more frequent rotations or land planted to groundnut could contribute to greater N inputs, but after household groundnut needs are met, there would need to be market opportunities to support greater production. Planting groundnut more frequently could lead to greater incidences of pest and disease, and advice from Uganda's NARO is to plant groundnut every three years or more to prevent such buildups (Okello et al., 2014). Households are already planting groundnut more frequently than this recommendation as ∼43% reported rotating groundnut every third season on the surveyed field. Farmers in the study area are land-limited as evidenced by the small field sizes, and 45% of farmers who intercropped said they did so because of limited land. Thus, expanding the area cropped to groundnut may not be feasible or meet household needs.

Groundnut yield increases are challenged by the fact that an estimated 80% of the groundnut seed is saved, may be of lower quality, and it is overwhelmingly from traditional, low-yielding varieties (Okello et al., 2010). However, there is a tradeoff between grain production and soil inputs because yield increases can lead to larger amounts of N exported in grain resulting in lower soil N balances, thus, in this regard, low-yielding varieties, and those that offer both moderate yields and abundant biomass, could be considered advantageous for soil fertility (Ojiem et al., 2007; Kermah et al., 2018). Crop yields and BNF are affected by climate and water availability, and within the study region, rainfall has been shown to be highly variable in its timing, and, while total rainfall has not changed significantly, the intra-seasonal distribution has (Hartter et al., 2012). Climate change and changes to the timing and distribution of rainfall heighten the uncertainty for all crop production, including groundnut, which in turn heightens the impact and importance of farmer management decisions and practices that can affect factors like soil moisture retention and nutrient availability.

CONCLUSIONS

Grain legumes like groundnut have the potential to contribute N-rich residues to boost SOC and TN and increase N available to other crops. Here, we estimated groundnut residue N delivery within minimal input, smallholder fields and found that there was a potentially substantial net N input at 70% BNF efficiency, but only if farmers retained residues on fields. However, after normalizing surveyed field soils using uncultivated reference soils from KNP, we did not find any evidence of differences in SOC or TN from fields where groundnut residues were retained vs. fields where they were removed. The high soil fertility inherent to the study area and the prevalence of diverse crop rotations, intercropping, and residue practices may have masked effects of residue management.

While our study focused on groundnut contributions to soil health, sustainability, and agricultural productivity, groundnut also provides essential nutrition and generates crucial income to support the health and well-being of smallholder farmers. Approximately half of the groundnut harvest in the surveyed fields was intended for household consumption, while ∼25% of the harvest was sold. Nutrient-rich groundnuts increase food security and diversify diets by providing protein, micronutrients, and phytochemicals to resource-poor households. Sale of groundnuts can generate high profits and bring in important income that may also contribute to food security. Though groundnut was second to maize in terms of household crop sales, households identified groundnut as the most profitable crop (34%) with maize a close second (31%). The majority of households (77%) categorized themselves as "very much" dependent on income from crop sales, thus groundnut generates vital income for these smallholder households.

Our study presents a valuable snapshot of a growing season, but multi-year studies are needed to fully assess the impact of legumes such as intercropped or rotated groundnut, as well as similar ecological nutrient management practices, on SOC and TN. There is a dearth of long-term studies examining the effects of grain legume rotations on SOM and soil properties in SSA. We recognize that there is a need to move beyond examination of legumes' potential benefits to soil and to institute trials to document changes over the long-term, including trials that collaborate with farmers to compare practices side-by-side on the same soils. Studies have mainly focused on changes in SOC and TN, as we did here, but we recommend quantification and analysis of more management sensitive, early indicators of SOC and N change, such as C and N within aggregates, and dissolved organic C and N. We used literature values to construct the N balance, and, in the process, we found few studies that examined groundnut plant total N, plant N partitioning, and N derived *via* BNF in farmer fields. We also did not find studies examining high plant population density and spacing effects on groundnut N uptake and BNF. Similarly, few studies examine the effects of farmer practices like removal, burning, incorporation, and surface spreading of groundnut residues on N retention in soil and N availability. Future research is needed to address these knowledge gaps, to gain a better understanding of groundnut's impact on soil fertility and to elucidate residue management practices that maximize short-term and long-term benefits to soils, human nutrition, and food systems within these smallholder contexts.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Michigan State University IRB. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

AW and LT devised the study and conducted the field work. AW performed the lab work, analyzed the data, and wrote the manuscript. LT contributed to interpretation of results and commented on the manuscript. All authors reviewed and approved the final manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2021.691786/full#supplementary-material

Supplementary Figure 1 | Potential single-season N balances for groundnut fields ($n = 77$) surveyed in 2015 in Kabarole district, western Uganda, accounting for belowground N input and N removal through grain harvest calculated at three BNF efficiencies, i.e., percentage groundnut plant N from BNF relative to total plant N demands, and grouped by residue management practice. Data are means ± one standard error.

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Integrating Social-Ecological and Political-Ecological Models of Agrobiodiversity With Nutrient Management of Keystone Food Spaces to Support SDG 2

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Agrobiodiversity—the biodiversity of food, agriculture, and land use—is essential to U.N. Sustainable Development Goal 2 by providing crucial food and nutritional quality of diets combined with strengthening agroecological sustainability. Focusing on the agrobiodiversity nexus to SDG 2, the current study utilized the interdisciplinary Agrobiodiversity Knowledge Framework (AKF), household-level surveys, and biodiversity sampling of crop fields and home gardens in a case study in Huánuco, Peru, in 2017. Statistical measures estimated agrobiodiversity of crop fields ($n = 268$ households) and home gardens ($n=159$ households) based on species richness (3.7 and 10.2 species/household, in fields and gardens, respectively) and evenness (Shannon diversity index; 0.70 and 1.83 in fields and gardens, respectively). Robust results of Poisson and OLS regression models identified several AKF-guided determinants of agrobiodiversity. Estimated species richness and evenness were significantly associated with 12 social-ecological and political-ecological factors from the four AKF thematic axes: farm characteristics and agroecology; diets and nutrition; markets, governance and sociocultural practices; and global change. This study's AKF approach, agrobiodiversity modeling, agroecological characterization, and field-based case study advanced a series of useful research insights, comparisons, and conceptual innovations to address SDG 2. Characterization of nutrient management through soil- and plant-focused cultural practices and livelihood roles distinguished the "keystone agrobiodiversity-and-food space" of multi-species maize fields (*maizales*) identified in AKF regression and characterization results. This key space furnished crucial food-nutrition and agroecological benefits that can be expanded by overcoming identified barriers. AKF-guided models incorporating key agrobiodiversity-and-food spaces and ecological nutrient management are needed to strengthen SDG 2 strategies.

Keywords: agricultural biodiversity, agroecology, Sustainable Development Goal 2, Agrobiodiversity Knowledge Framework, key agrobiodiversity-and-food spaces, political ecology, social-ecological systems, Peru

INTRODUCTION

Actively addressing global hunger and malnutrition as urged in U.N. Sustainable Development Goal 2 ("Zero Hunger;" hence SDG 2) requires vital, diverse dietary and nutritional inputs derived from the biodiversity of food, agriculture, and land use (agrobiodiversity). This human-managed biodiversity functions in a nexus role between food-nutrition needs and agroecology. Agrobiodiversity bridges both the access to food and nutrition (Foote et al., 2004; Frison et al., 2011; Fanzo et al., 2013; Jones et al., 2018; Lachat et al., 2018; Williams et al., 2018; CIP, 2019; Zimmerer et al., 2020) and the complex of agroecological, ecosystem-service, adaptive, and social- and political-ecological dynamics (Jackson et al., 2007; Jarvis et al., 2007; Pascual et al., 2011; Zimmerer et al., 2019; Gerits et al., 2021; Labeyrie et al., 2021). Focus on the links of agrobiodiversity to SDG 2 is central to socially just, nutritious food systems (Zimmerer and de Haan, 2020) and sustainable development (Gepts et al., 2012; Kremen et al., 2012; Vandermeer et al., 2018; Martin et al., 2019; Willett et al., 2019; Zimmerer et al., 2021). This study uses this focus to prioritize empowering poor and marginalized indigenous and smallholder populations.

The interdisciplinary Agrobiodiversity Knowledge Framework (AKF; Smale et al., 2006; precursors in Smale, 2006; Zimmerer and de Haan, 2019; Zimmerer et al., 2019, 2020) guides this study's focus on the agrobiodiversity nexus with SDG 2 and agroecological nutrient management. As shown (**Figure 1A**), the AKF integrates dynamics of: (1) farms and agroecology; (2) food, nutrition, and diets (food practice, food/nutrition security, health, and SDG2); (3) social/socioeconomic and cultural factors (markets, governance, and cultural practices including livelihood facets and biocultural sub-models); and (4) global changes (climate change, national-international markets, programs, and policies). The AKF model guiding this study thus expands predominant farm-environment approaches.

The four AKF themes (**Figure 1A**) reflect expanding research on agrobiodiversity in relation to dietary, nutrition, and health to address hunger and disease (Foote et al., 2004; Frison et al., 2011; Fanzo et al., 2013; Jones et al., 2018; Lachat et al., 2018; Williams et al., 2018; Downs et al., 2020). The AKF expands emphasis on biodiversity conservation of crop and genetic resources (Brush, 2000; Gepts et al., 2012; Bellon et al., 2015) in conjunction with growing recognition of food and nutrition benefits as well as biocultural dynamics and sustainable development that include human rights and livelihoods (Caillon et al., 2017; Zimmerer and de Haan, 2017, 2019). Additionally, the AKF incorporates agroecological characterization and functions in global-change contexts (e.g., Wood et al., 2015; Zimmerer et al., 2019) including social-ecological and political-ecological transitions (Jackson et al., 2012; Toledo and Barrera-Bassols, 2017; Bottazzi and Boillat, 2021; Goldberg et al., 2021; Labeyrie et al., 2021).

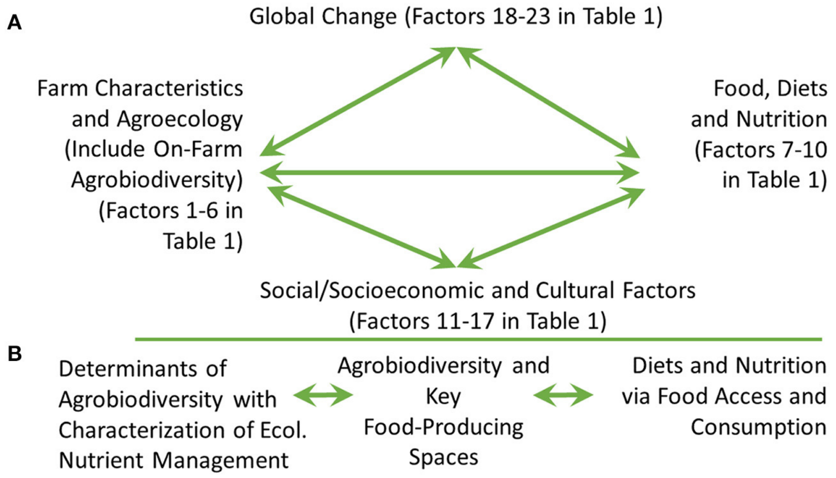

FIGURE 1 | (A) Conceptual model of themes of the Agrobiodiversity Knowledge Framework (AGK) with reference to enumerated factors in **Table 1**. These AKF themes are linked to the specific factors in **Tables 2–4**, with the illustrated AKF themes in this figure and the referenced factors serving as the connecting thread through the tables, text, and analysis. **(B)** Overview of agrobiodiversity-SDG research of this study (left-center) and related project (center-right).

This study addresses questions concerning the nexus roles of agrobiodiversity amid dynamically changing conditions: (1) which AKF-identified factors drawn from social-ecological systems and political ecology (**Figure 1A** and **Table 1**) are associated with the variation of agrobiodiversity? (noting the latter are crucial to nutrition outcomes; Jones et al., 2018; Zimmerer et al., 2020) (2) what keystone food-generating spaces contribute to agrobiodiversity outcomes and what influences their occurrence? (3) what is the preliminary characterization of ecological nutrient management in these key spaces? and (4) how can both comparability of results and new concepts of agrobiodiversity be advanced for SDG 2?

The overarching goal is to strengthen broad, nimble sustainability-enhancing capacities (sensu Petersen-Rockney et al., 2021) that can generate solutions to SDG-2 by integrating the AKF, socio-ecological modeling, and "keystone agrobiodiversity-and-food spaces" with ecological nutrient management. The study's distinct focus (**Figure 1A** and thickened arrow on left center of **Figure 1B**) is integrated with our overarching SDG 2-centered research on dietary diversity and nutrition wellbeing linked to agrobiodiversity (Jones et al., 2018) as well as current food and livelihood struggles (Zimmerer et al., 2020). The relations of this study to overarching research and earlier studies are reflected in the right-center of **Figure 1B**.

This study uses the AKF and existing research to identify potential social- and political-ecological determinants (**Table 1**, 1st column) in each of the four AKF themes (**Table 1**, 2nd column; also **Figure 1A**). Factors are hypothesized to influence agrobiodiversity *via* specific processes (3rd column) and examples of conditional interaction webs (4th column). Each factor is rooted in extensive research utilizing agrobiodiversity regression analyses (5th column).

AKF-based design and testing statistical models of social- and political-ecological predictors, as undertaken here, draw on anticipated influences of economics, development, and policy (Van Dusen and Taylor, 2005; Smale, 2006; Smale et al., 2006; Di Falco et al., 2010; Pascual et al., 2011; Rahman and Kazal, 2015; Garduño and Perrings, 2020; Goldberg et al., 2021). AKF-based consideration of model factors draws also from demonstrated influences of culture and society (Williams and Kramer, 2019), social-ecological systems and political ecology (Williams, 2016), and agroecology (see above). The AKF models developed here seeks to engage and advance these approaches.

This study develops an original approach toward culturally managed "keystone agrobiodiversity-and-food spaces" that can range from crop fields and home gardens to food-generating "wild" spaces (Nabhan, 2012, 2018). Currently, these spaces are being transformed amid intensified livelihood integration with extra-local product and labor markets as well as state- and non-state programs and projects (Zimmerer et al., 2020, 2021). Evolving spatial complexity requires identification and analysis of this dimension of agrobiodiversity's role in SDG 2.

Finally, this study engages expanding agroecological focus on ecological nutrient management (Fonte et al., 2012; Vanek et al., 2020) to offer preliminary results on key agrobiodiversity-and-food spaces. It focuses on field fallow and crop rotation as major management strategies (Arce et al., 2019a,b) as well as principal groups of cultivated and managed plants related to soil-nutrient management (Smil, 1997; Schipanski and Drinkwater, 2012; Pérez-Garcia and del Castillo, 2016; Meena and Lal, 2018). It suggests future linking of agrobiodiversity and agroecological research through integrating the AKF, socio-ecological modeling, and key food spaces with ecological nutrient management.

MATERIALS AND METHODS

Study Area of Huánuco, Peru: Combined "Bright Spot" and "Hot Spot" of Agrobiodiversity

Huánuco, Peru, is marked by complex relations of food, nutrition, and agrobiodiversity (**Figure 2**; Malice et al., 2010; Velásquez-Milla et al., 2011; Jones et al., 2018; Zimmerer et al., 2020). Climate, topography, soils, and environmental diversity of Huánuco are representative of valley-upland regions of the Andes Mountains in Peru (Pulgar Vidal, 1996, p. 225) and western South America. The Huánuco Andes extend to ecotones of the Upper Amazon. This "bright spot" of agrobiodiversity (sensu Gould et al., 2021) is also a "hotspot" subject to dynamic agri-food changes including widespread food and nutrition insecurity (Zimmerer et al., 2020) where policy legacies and land privatization (Mayer, 2009) contribute to the urgent need to address SDG 2. Social-ecological and political-ecological drivers of agrobiodiversity change in Huánuco are characteristic of the Andes, Amazon, and global trends (de Haan et al., 2010; Oyarzun et al., 2013; Skarbø, 2014; Arce et al., 2019b; de Haan, 2021; Zimmerer et al., 2021).

This study was sited in three Huánuco landscapes (Quishqui, Amarilis-Malconga, and Molinos-Umari; **Figure 2**) that are environmentally and socially distinct. Census and municipal-level data guided the structured-random selection of 10 communities with similar elevation-range characteristics in each landscape. 20 households were then randomly selected to participate out of the 25–40 households in study communities. Eligible households met the following inclusion criteria: (1) members were permanent residents of the household, (2) a woman aged 15–49 years was a household member, and (3) field and/or garden crops had been cultivated by one or more members in 2016–17. For the household survey, we sampled 20 households per community. The selected communities had 25–40 households while extremely small communities were excluded. Institutional human subject approvals (IIN in Lima, Peru, and University of Michigan) guided informed consent and research ethics protocols.

Household Survey

We administered a multi-module household survey to the 600 participating households (April–June 2017) that collected data on potential co-variates with agrobiodiversity. It included

TABLE 1 | Hypothesized social-ecological and political-ecological determinants of agrobiodiversity based on the Agrobiodiversity Knowledge Framework (AKF); data sources for variables refer to survey as "S" and agrobiodiversity sampling as "AS" (descriptions in text).

Variable (with measure) and data source	**AGK concept category and added details of variable (if needed)**	**Hypothesized immediate influence**	**Interacting factors in potential pathways AND Webs**	**Supporting research (regression models of agrobiodiversity and select non-regression studies)**
1) Areas of total cultivated area and fields only (hectares) (AS)	Farm Chars. and Agroecol.	Households with more planting area (both overall and field space only) are enabled to produce higher levels of agrobiodiversity (+)	Demographic change and influences of population and land-access reforms of the Peruvian state including policies and political economy	Ban and Coomes, 2004; Abay et al., 2009; Di Falco et al., 2010; Velásquez-Milla et al., 2011; Oyarzun et al., 2013; Skarbø, 2014; McCord et al., 2015; Obayelu et al., 2015; Arce et al., 2019a,b; Dessie et al., 2019; Williams and Kramer, 2019; Goldberg et al., 2021; Li et al., 2021
2) Field number (count) (AS)	Farm Chars. and Agroecol.	More fields enable households to produce higher agrobiodiversity (+)	See above	Benin et al., 2004; Coomes and Ban, 2004; Van Dusen and Taylor, 2005; Dessie et al., 2019
3) Elevation and Elevation Range (masl) (AS)	Farm Chars. and Agroecol.	Elevations of residence and/or across range of fields can enable higher agrobiodiversity (+)	See above	Van Dusen and Taylor, 2005; Abay et al., 2009; Mercer and Perales, 2010; Arce et al., 2019a,b
4) Legume crop rotation (LCR index[a]) (AS)	Farm Chars. and Agroecol.	Enhances soil fertility and nutrient availability for agrobiodiverse plants (+)	Multi-factor decision-making about crop choice; agroecological awareness and support	Smil, 1997; Benin et al., 2004; Di Falco et al., 2010; Meena and Lal, 2018
5) Garden Presence/Absence and Area (hectares) (AS)	Farm Chars. and Agroecol.	Enables household to maintain seeds and production knowledge for agrobiodiversity(+)	Space and resources (time, growing environment) near house	Ban and Coomes, 2004; Wezel and Ohl, 2005; Perrault-Archambault and Coomes, 2008; Williams and Kramer, 2019
6) Multi-Species Maize Field (pres./abs.) (AS)	Farm Chars. and Agroecol.	Enables household to maintain seeds and production knowledge for agrobiodiversity (+)	Space and resources (time, growing environment) near house	Velásquez-Milla et al., 2011; Skarbø, 2014; Novotny et al., 2021
7) Self-Produced Food in Diet (calories) (S)	Food; Refers to diet of adult woman individual (see text)	A household's greater reliance on self-produced food increases agrobiodiversity (+)	Influenced by combined self-production and marketing rationales	Velásquez-Milla et al., 2011; Oyarzun et al., 2013; Nordhagen et al., 2017; Williams and Kramer, 2019; Li et al., 2021
8) Traditional- Foods (S)	Food; Calories of traditional foods in diet of adult woman individual	Greater reliance on traditional foods in diet leads to higher agrobiodiversity (+)	Influenced by choices and capacity to utilize traditional food	Oyarzun et al., 2013; Skarbø, 2014; Nordhagen et al., 2017; Li et al., 2021
9) Dietary Diversity (MDDW Achieved or Not Achieved) (S)	Food; Refers to diet of adult woman individual (see text)	Greater expectation and familiarity with dietary diverse can increase production of agrobiodiversity (+)	Potential influence on agrobiodiversity production through awareness and valuation	Fanzo et al., 2013; Oyarzun et al., 2013; Nordhagen et al., 2017; Li et al., 2021
10) Food Security (S)	Food; Refers to all household members	Food-secure households access foods associated with higher production agrobiodiversity (+)	Potential influence on agrobiodiversity production through awareness and valuation	Frison et al., 2011; Fanzo et al., 2013; Nordhagen et al., 2017; Zimmerer and de Haan, 2020
11) Age (head of household) (AS)	Social/socio-economic and cultural factors	Older heads of households manage knowledge, food preferences, and production portfolios associated with higher agrobiodiversity (+)	Demographic factors such as migration of young adults can influence the prevalence of elderly in rural communities	Benin et al., 2004; Van Dusen and Taylor, 2005; Perrault-Archambault and Coomes, 2008; Abay et al., 2009; Ng'endo et al., 2015; Williams, 2016; Dessie et al., 2019; Williams and Kramer, 2019; Gauchan et al., 2020; Li et al., 2021
12) Gender (head of household) (AS)	Social/socio-economic and cultural factors	Women heads of households manage identity practices, knowledge, food preferences, and production portfolios associated with higher agrobio-diversity (+)	Demographic factors such as migration of male adults can influence the prevalence of women-headed households in rural communities	Benin et al., 2004; Momsen, 2007; Perrault-Archambault and Coomes, 2008; Abay et al., 2009; Di Falco et al., 2010; Whitney et al., 2018; Dessie et al., 2019
13) Ethnicity and Language (main language Quechua) (S)	Social/socio-economic and cultural factors	Ethnic identity associated with language can co-occur with cultural practices of high agrobiodiversity (+)	Ethnicity and language are active practices influenced by large webs of factors that include politics of indigeneity	Brush and Perales, 2007; Reyes-García et al., 2008; Velásquez-Milla et al., 2011; Labeyrie et al., 2016; Orozco-Ramírez et al., 2016; Williams, 2016; Whitney et al., 2018; Williams and Kramer, 2019

(Continued)

TABLE 1 | Continued

Variable (with measure) and data source	AGK concept category and added details of variable (if needed)	Hypothesized immediate influence	Interacting factors in potential pathways AND Webs	Supporting research (regression models of agrobiodiversity and select non-regression studies)
14) Household income (soles/year) (S)	Social/socio-economic and cultural factors	Greater household income can lead to planting options that either include or exclude agrobiodiversity (+/-)	Household income reflects socioeconomic assets and policy factors acting on market integration	Zimmerer, 1991, 1996; Benin et al., 2004; Coomes and Ban, 2004; McCord et al., 2015; Ng'endo et al., 2015; Obayelu et al., 2015; Williams, 2016; Zimmerer et al., 2020; Goldberg et al., 2021; Li et al., 2021
15) Social capital (see text) (S)	Social/socio-economic and cultural factors	More and stronger networks and other forms of social capital can either include or exclude agrobiodiversity (+/-)	Networks and other social capital reflect economic capacities, social power relations, and combined politics and micro-politics	Obayelu et al., 2015; Labeyrie et al., 2016; Williams, 2016; Wale and Holm-Mueller, 2017
16) Geographic sub-area (place) (see Methods) (AS)	Social/socio-economic and cultural factors	Geographic sub-area (place) exerts influence through place-based configurations of multiple factors (+/-)	Place-based differences affecting agrobiodiversity arise from local and extra-local forces	Zimmerer, 1991, 1996; Smale et al., 2001; Williams and Kramer, 2019
17) Level of Education (S)	Social/socio-economic and cultural factors	Education level can lead to either higher or lower agrobiodiversity (+/-)	Education effects can drive changed valuation of agrobiodiversity	Gauchan et al., 2005; Van Dusen and Taylor, 2005; Abay et al., 2009; Skarbø, 2014
18) Distance to major urban center (kms) (AS)	Global change	Urban centers expected to exert pressures for market integration and other changes reducing agrobiodiversity levels (–)	Interpretation of distance-to-city effects often assume distance decay model of reduced influence	Benin et al., 2004; Wezel and Ohl, 2005; Perrault-Archambault and Coomes, 2008; Di Falco et al., 2010; Williams, 2016; Conrad et al., 2017; Whitney et al., 2018; Dessie et al., 2019
19) Reliance on agrochemical inputs in field cultivation (S)	Global change; household's number fields with chemical fertilizer use	Modern agricultural inputs including chemical fertilizers reduce agrobiodiversity viability (-)	Agricultural modernization reflects diverse socioeconomic and sociocultural influences	Velásquez-Milla et al., 2011; Dedeurwaerdere and Hannachi, 2019
20) Current participation in programs and projects of government agencies and NGOs (S)	Global change; number of extra-local programs in which household participated	Program influences, ranging from agricultural extension, can either reduce or increase agrobiodiversity (+/-)	Presence and role of programs results from diverse state and non-state actors and organizations	Abay et al., 2009; Williams, 2016; Wale and Holm-Mueller, 2017; Mwololo et al., 2019
21) Degree of commercialization (S)	Global change; percent of household's crop harvest sold (2017)	Market integration of agricultural production may reduce or increase agrobiodiversity (+/-)	Integration into agricultural markets reflects multi-factor web of influences	Van Dusen and Taylor, 2005; Skarbø, 2014; Obayelu et al., 2015; Dedeurwaerdere and Hannachi, 2019
22) Climate and climate change (adaptative responses) (S)	Global change; number of household's adaptions	Climate change impacts can reduce or increase agrobiodiversity (+/-)	Climate change pressures to increase agrobiodiversity include adaptations	Abay et al., 2009; Mercer and Perales, 2010; Bhattarai et al., 2015; McCord et al., 2015; Saxena et al., 2016; Arce et al., 2019a,b; Zimmerer et al., 2019
23) Agrobiodiversity loss awareness (household head) (S)	Global change; number of elements indicated by household head	Awareness of agrobiodiversity loss can be associated with familiarity (-) or conservation (+)	Awareness of agrobiodiversity loss can arise in individual, family, community, and extra-community contexts	Smale et al., 2001; Wale and Holm-Mueller, 2017; Dedeurwaerdere and Hannachi, 2019

[a] *Estimated as the sum of the frequencies of legume-containing fields observed in the 2017 sample and recollected in the field-level histories of crop rotation (2013–2017).*

modules on sociodemographic characteristics, livelihood assets, food security, dietary intake, and livelihood activities, among other topics.

In addition, a quantitative 24-h recall of food intake of the young or medium-age woman used the multiple-pass method (Gibson, 2005). One hundred women from this sample were randomly selected for a second food intake recall interview after the first interview. From recall data, a 10-food group diet diversity score was used to calculate the Minimum Dietary Diversity for Women (MDD-W) indicator, defined as 1 if the respondent consumed five or more food groups in the previous 24 h and 0 otherwise (Martin-Prevel et al., 2015; FAO, 2016). A 15 g minimum cut-off defined consumption of a given food group. Information on co-variates obtained through above methods is marked with "S" in **Table 1** (1st column).

Agrobiodiversity Sampling and Diversity Estimations

One half of surveyed households ($n = 300$) were randomly selected to participate in sampling agrobiodiversity. Most households cultivated fields ($n = 268$) and about one half produced gardens ($n = 159$) as sites for combined market production and home food consumption. The household's principal food-producing spaces were visited with members

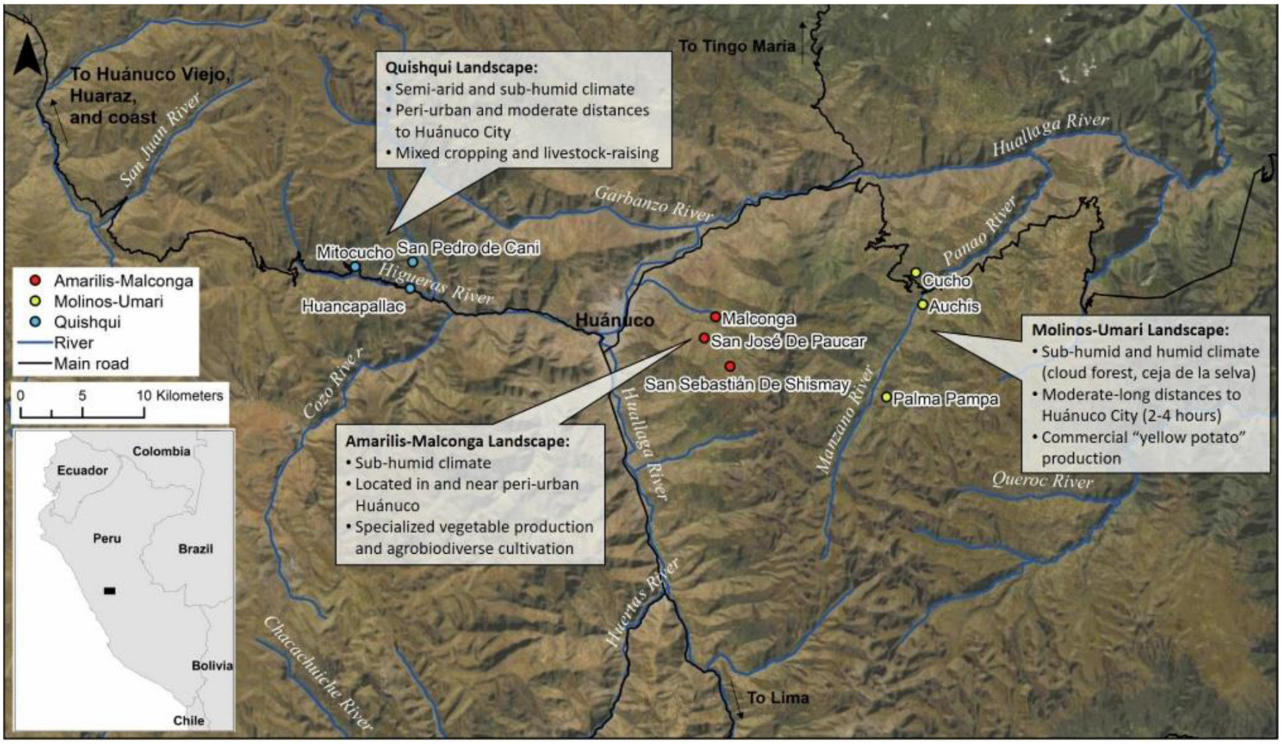

FIGURE 2 | Map of Huánuco study area in Central Peru, with examples of participating study communities in research-focus landscapes (Quishqui, Amarilis-Malconga, Molinos-Umari).

that participated in sampling (Agrobiodiversity Sampling, AS) using local-name identification and spatial sub-areas. Species-level scientific identification of AS taxa was overseen by local agrobiodiversity experts at the Universidad Nacional Hermilio Valdizan in Huánuco. AS incorporated information on the major food-generating spaces of each household (e.g., rotation history, ownership, and type such as field or garden. These co-variate data are marked "AS" in **Table 1** (1st column).

Household-level diversity estimates derived from AS data for fields ($n = 268$ households) and gardens ($n = 159$ households) subsequently were used in regression models described below. Our diversity-estimation approach cites specific works since focus on the species level requires general justification (Colwell, 2009: 258; Magurran, 2013; Williams, 2016; Jones, 2017; Zimmerer et al., 2020; Goldberg et al., 2021) and is used specifically to distinguish key food spaces in this study. This species-level focus complements existing agrobiodiversity estimation of cultivars, varieties, and landraces (Smale et al., 2001; Obayelu et al., 2015; Wale and Holm-Mueller, 2017; Dedeurwaerdere and Hannachi, 2019; Gatto et al., 2021), genetic populations (de Haan et al., 2010; Perronne et al., 2017; Arce et al., 2019a,b), and landscapes (Zimmerer et al., 2020), as well as agroecological functional diversity addressed below.

Richness (a count statistic of the number of cultivated and managed food-producing species) and the Shannon diversity index ($\mathrm{H} = - \sum_{s}^{i=1} p_i \ \ln \ \mathrm{p}_i$) (Colwell, 2009, p. 260)—the latter is an estimate of the relative abundances of species referred to as evenness—were chosen as twin statistical estimates of agrobiodiversity [for statistical formulas, symbols, and rationales see Colwell (2009), Magurran (2013), Smale (2006)]. These diversity measures are widely used individually and in combination for agrobiodiversity research (Benin et al., 2004; Jarvis et al., 2008; Oyarzun et al., 2013; Williams, 2016; Jones et al., 2018; Goslee, 2020; Goldberg et al., 2021) as well as "wild" biodiversity (Colwell, 2009; Hayek and Buzas, 2010). Biodiversity estimates of richness and evenness were visualized on maps and graphs (**Figure 5** in Results).

We calculated additional agrobiodiversity estimates using information statistics of the Margalef and Menhinick indices ($\mathrm{D_{Mg}} = \mathrm{(S\text{-}1)/(ln\ N)}$ and $\mathrm{D_{Mn}} = \mathrm{S}/\sqrt{\mathrm{N}}$, respectively) and alternative evenness measures (modified Shannon diversity index, $\mathrm{H'} = \mathrm{e^H}$ and two forms of the Simpson diversity index, $\mathrm{D} = 1 - \sum_{i=1}^{s} p_{\mathrm{i}}^{2}$ and $\mathrm{D'} = (\sum_{i=1}^{s} p_{\mathrm{i}}^{2})^{-1}$ (Smale, 2006; Colwell, 2009, p. 260; Magurran, 2013). These additional biodiversity estimates (**Supplementary Tables 1, 2**) were important though less central to this study and less common in existing agrobiodiversity research. Functional diversity, defined as the diversity of species niches or functions (Villéger et al., 2008; Finney and Kaye, 2017; Blesh, 2018), shown elsewhere as complexly related to agroecological multi-functionality (Blesh, 2018), is treated in this study as important general information. Preliminary distinctions of plant functional groups and nutrient management, described methodologically below, suggests a promising area where future research can more fully integrate functional diversity and agroecology as outlined in the Discussion.

TABLE 2 | Estimations of the social-ecological and political-ecological factors of the Agrobiodiversity Knowledge Framework (AGK) in the sample utilized for the regression analysis of fields.

Factor	AKF category	*N* (households)	Mean value	Standard deviation	Range
Crop species richness (fields)	Dependent variable	268	3.7	2.9	1, 24
Crop species evenness (Shannon index) (fields)	Dependent variable	268	0.70	0.52	0, 2.25
Crop species richness (gardens)	Dependent variable	159	10.2	6.3	1, 33
Crop species evenness (Shannon index) (gardens)	Dependent variable	159	1.83	0.65	0, 3.2
Extent of total cultivated area (hectares)	Farm-agroeco	300	0.404	0.036	0.009, 2.45
Extent of total cultivated area of fields (hectares)	Farm-agroeco	268	0.426	0.036	31, 2.39
Extent of total cultivated area of garden (hectares)	Farm-agroeco	159	0.0452	0.0093	0.0086, 0.8367
Number of cultivated fields (count)	Farm-agroeco	300	2.5	1.5	1, 11
Elevation of residence (masl)	Farm-agroeco	300	2650	436	1840, 3885
Elevation range of fields (masl)	Farm-agroeco	300	50	100	0, 625
Legume crop rotation index (defined in **Table 1**)	Farm-agroeco	300	0.60	0.62	0, 2
Garden presence/absence and area (square meters)	Farm-agroeco				
No garden		141	47.0%		
Garden		159	53.0%		
Multi-species maize field (pres./abs.)	Farm-agroeco				
No		154	51.3%		
Yes		146	48.7%		
Self-produced food in diet (% calories self-production)	Food	300	36.5	22.7	0, 100
Traditional foods in diet (% calories from traditional foods)	Food	300	34.2	17.7	0, 89.4
Dietary diversity (MDDW achieved/not-achieved)	Food				
Achieved		137	45.7%		
Not-Achieved		163	54.3%		
Food security	Food				
Food insecure		176	58.7%		
Food secure		124	41.3%		
Age (head of household)	Social/socio-economic and cultural factors	300	49.8	16.7	21, 120
Gender (head of household)	Social/socio-economic and cultural factors				
Male		228	76.0%		
Female		72	24.0%		
Ethnicity and language (primary language Quechua)	Social/socio-economic and cultural factors				
Primary language not Quechua (reference)		100	33.3%		
Primary language Quechua		200	66.7%		
Household income (soles/year)	Social/socio-economic and cultural factors	300	3,571	8,629	0, 128,000
Social capital (sum of indicators)	Social/socio-economic and cultural factors	300	2.8	2.0	0, 13

(Continued)

TABLE 2 | Continued

Factor	AKF category	*N* (households)	Mean value	Standard deviation	Range
Geographic sub-area (place)	Social/socio-economic and cultural factors				
Quisqui		100	33.3%		
Amarilis		100	33.3%		
Molinos		100	33.3%		
Level of education	Social/socio-economic and cultural factors				
No education		34	11.5%		
Incomplete primary		114	38.5%		
Complete primary		64	21.6%		
Incomplete secondary		41	13.9%		
Complete secondary		41	13.9%		
Post-secondary		2	0.68%		
Numbers of fields with chemical fertilizer use	Global change	300	0.64	0.77	0, 4
Degree of commercialization (% marketed)	Global change	267	42.4	36.8	0, 100
Climate and climate change (number adaptations) (0–6)	Global change	300	2.67	1.5	0, 8
Agrobiodiversity loss awareness (1–5)	Global change	300	1.22	1.14	0, 5

Descriptive Statistics and Regression Analysis

Descriptive statistics assessed the hypothesized predictive factors, with calculations of mean, standard deviation and range of each hypothesized determinant and dependent variable (**Table 2** in Results). We then applied multiple regression analysis using Stata statistical software package, version 15.1 (2018; StataCorp) to determine associations of AKF-hypothesized determinants with the four dependent variables (crop species richness of crop fields and home gardens, and Shannon diversity index of crop fields and home gardens).

Poisson regressions were fit to main models regressing covariates on cultivated species richness of crop fields and home gardens (**Tables 3**, **4** in Results). Values are reported as incidence rate ratios (IRR) where a one-unit increase in the independent variable is associated with a percentage increase in the dependent variable based on the IRR (e.g., an IRR of 1.08 equates to an 8% dependent-variable increase). **Table 1** describes each independent variable in these models including its hypothesized process of influence on the dependent variables.

Ordinary least-squares regressions were fit to main models regressing covariates on the Shannon diversity index (**Tables 3**, **4** in Results) in addition to supplementary models using the additional biodiversity indices (**Supplementary Tables 1, 2**). "Distance" and "current participation in programs" were assessed as AKF-guided independent variables although subsequently omitted since they were found to be statistically insignificant and, due to data limitations, would reduce the utilizable sample of households in regression models. Independent variables used in the garden models differed slightly from the models of crop-field agrobiodiversity, with extent of total garden cultivated area substitute for extent of total cultivated field. The variables "presence of a garden" and "fields with chemical fertilizer use" were omitted in the garden-agrobiodiversity regressions.

Associations of predictor factors and diversity indices were considered consistent with random variability at $P > 0.05$ (Fisher, 1950, p. 80), with coefficients, Standard Error (SE) and P-values reported in **Tables 3**, **4** in Results. In addition, a supplement of 16 regression sub-models for grouped AKF factors (farm characteristics and agroecology; diets and nutrition; governance; global change) were estimated for crop fields (**Supplementary Tables 3–6**) and home gardens (**Supplementary Tables 7–10**). Breaking out hypothesized factors into sub-models was used to check for possible over-parameterization in the main models. Only factors determined statistically significant in both the main models and supplementary sub-models are reported and discussed below.

Characterization of Keystone Agrobiodiversity-and-Food Spaces

Ecological nutrient management and livelihood roles were estimated for key landscape spaces of agrobiodiversity and food production. Nutrition-focused analysis (Jones et al., 2018; Zimmerer et al., 2020) has signaled the importance of both crop fields (locally *chakras* or *parcelas*) and home gardens (kitchen or dooryard gardens, locally *huertos*). Initial field research involving visits with Huánuco food-growers undertaken in 2017 indicated the potential importance of multi-species maize fields (locally *maizales*) as an additional distinct type specified further in regression results and fieldwork (Results, **Tables 2–4**, **Figure 8**).

Preliminary characterization of ecological nutrient management utilized the AS data to estimate uncultivated fallow (2011–2017), crop rotation (2013–2017), and multi-species

TABLE 3 | Results of multiple regression analyses of the associations of social-ecological and political-ecological factors with crop species agrobiodiversity in fields (*Chakras*, *Parcelas*).

Factor	Richness incidence rate ratio (standard error)	*P*-value	Shannon evenness coefficient (standard error)	*P*-value
Extent of total cultivated area (hectares)	1.00 (0.0000779)	0.48	−0.00004 (0.0000721)	0.583
Extent of total cultivated area of fields (hectares)	0.99 (0.0000795)	0.208	0.00002 (0.0000732)	0.818
Number of cultivated fields (count)	1.26*** (0.0288)	0.000	0.17*** (0.0240)	0.000
Elevation of residence (masl)	1.00 (0.000117)	0.586	0.00008 (0.0000893)	0.382
Elevation range of fields (masl)	1.00 (0.000364)	0.457	−0.0004 (0.000299)	0.155
Legume crop rotation index (**Table 1**)	1.18* (0.0699)	0.019	0.11* (0.0532)	0.037
Garden presence				
Garden not present (reference)				
Garden present	0.64*** (0.0862)	0.000	−0.16* (0.0674)	0.020
Multi-species maize field				
No multi-species maize field				
Multi-species maize field present	1.76*** (0.0830)	0.000	0.45*** (0.0627)	0.000
Self-produced food in diet	0.83 (0.288)	0.521	0.04 (0.228)	0.852
Traditional foods in diet	0.99 (0.00330)	0.398	−0.002 (0.00261)	0.490
Dietary diversity				
MDDW not achieved				
MDDW achieved	0.98 (0.0776)	0.752	0.07 (0.0602)	0.225
Household food security status				
Food insecure (reference)				
Food secure	0.94 (0.0746)	0.433	−0.08 (0.0569)	0.182
Age (head of household)	0.99 (0.00247)	0.973	0.0007 (0.00191)	0.721
Gender (head of household)				
Male (reference)				
Female	0.97 (0.0896)	0.719	−0.04 (0.0706)	0.534
Ethnicity and language				
Primary language not Quechua (reference)				
Primary language Quechua	1.20 (0.0965)	0.060	0.10 (0.0736)	0.169
Household income (soles/year)	0.99 (0.00000483)	0.250	-2.7×10^{-6} (0.00000295)	0.354
Social capital (sum of indicators)	1.04 (0.0182)	0.057	0.002 (0.0144)	0.870
Geographic sub-area (place)				
Quisqui (reference)				
Amarilis	0.89 (0.0920)	0.219	−0.02 (0.0715)	0.818
Molinos	0.87 (0.0971)	0.151	−0.19* (0.0747)	0.013
Level of education (head of household)				
No education (reference)				

(Continued)

TABLE 3 | Continued

Factor	Richness incidence rate ratio (standard error)	*P*-value	Shannon evenness coefficient (standard error)	*P*-value
Incomplete primary	0.91 (0.108)	0.396	−0.0 8 (0.0903)	0.403
Complete primary	0.90 (0.127)	0.400	−0.10 (0.104)	0.324
Incomplete secondary	0.77 (0.139)	0.066	−0.10 (0.111)	0.384
Complete secondary	0.97 (0.144)	0.833	−0.05 (0.115)	0.644
Post-secondary	3.85^{**} (0.415)	0.001	0.79 (0.440)	0.073
Fields with chemical fertilizer use	1.05 (0.0480)	0.358	−0.04 (0.0379)	0.237
Degree of commercialization (agricultural fields)	0.99 (0.00116)	0.663	0.0007 (0.000905)	0.464
Climate and climate change (number adaptations)	1.01 (0.0261)	0.667	0.02 (0.0195)	0.241
Agrobiodiversity loss awareness	1.00 (0.0339)	0.889	−0.01 (0.0265)	0.617
Pseudo R^2	0.16 R^2			0.45

Values for the model with richness as the dependent variable are incidence rate ratios (IRRs) from Poisson regressions adjusting for the other covariates shown. Values for the model with Shannon Evenness as the dependent variable are partial regression coefficients from OLS regressions adjusting for the other covariates shown. n = 245 for both models. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

plantings (2017). Additionally, AS data enabled categorizing plants in relation to management of soil nutrients and general soil maintenance: (1) nitrogen-fixing legume crops for food and forage; (2) woody vegetation and perennials with generally more extensive root zones; and (3) maize that functions as an extensively rooted annual species. Identification of plant-group categories reflects agroecological, agronomic, and soils research on ecological nutrient management (Smil, 1997; Schipanski and Drinkwater, 2012; Meena and Lal, 2018) as well as research on these plant groups utilized in soil and nutrient management in the Andes (Fonte et al., 2012; Vanek et al., 2020). The total of six above-mentioned agroecological management techniques and plant groups were determined as preliminary estimates feasible using the AS data that had been collected primarily for taxonomic biodiversity estimates. Potential expansion of future social-ecological and political-ecology research on agrobiodiversity to include agroecological methods is described in the Discussion.

Additionally, food and income, which serve major livelihood roles (Arce et al., 2019b; Zimmerer et al., 2020), were characterized based on proportional inputs relative to overall self-produced food and overall farm income, respectively. A group of five key informants knowledgeable about local food, agriculture, and livelihoods rated each farm space from "1 = very important" to "5 = notably unimportant."

RESULTS

Agrobiodiversity and Descriptive Statistics

Agrobiodiversity sampling (AS) and identification resulted in a total of 92 cultivated species in crop fields (**Figure 3**). Most frequent among households were maize (Zea mays, *maíz*; 65.02%), Andean common beans (Phaseolus vulgaris, *frejol*; 34.98%), potatoes (Solanum tuberosum, *papa*; 29.37%), Andean squashes (Cucurbita maxima, *zapallo*, and Cucurbita ficifolia, *calabaza*; 29.04%), and fava beans (Vicia faba, *habas*; 18.81%). Home gardens showed 146 species of agriculturally managed plants (**Figure 4**). Most frequent were onion (Allium cepa, *cebolla*; 46.47%), oregano (Origanum vulgare, *orégano*; 40.59%), cilantro (Coriandrum sativum, *culantro*; 38.24%), peach (Prunus persica, *durazno*; 34.71%), and *chincho* (Tagetes elliptica; 32.94%). The species-frequency curves of both crop fields and home gardens were inverse exponential relationships (**Figures 3**, **4**).

Richness of field crops based on agrobiodiversity sampling (AS) with 268 households (**Table 2**) averaged 3.7 cultivated species/household with the range of 1–24 species. Mean richness of agriculturally management plants in home gardens was 10.2 species per household with a range of 1–33 species (**Table 2**). Results showed the mean of 7.9 species for all households. This estimated total agrobiodiversity richness, as well as field- and garden-level estimates, did not vary significantly among the three study landscapes. Mapping the species-level richness of agrobiodiversity (combined fields and gardens) illustrated the notable occurrence of household-level variation and the lack of geographic patterning or clustering either within or among the study landscapes (**Figure 5**). Mean values of the Shannon diversity index were estimated as 0.70 and 1.83 for the cultivated and managed species of crop fields and home gardens, respectively.

TABLE 4 | Results of multiple regression analyses of the associations of social-ecological and political-ecological factors with managed species agrobiodiversity in gardens (*Huertos*, *Huertas*).

Factor	Richness incidence rate ratio (standard error)	*P*-value	Shannon Evenness coefficient (standard error)	*P*-value
Extent of total cultivated area (hectares)	0.99 (0.0000120)	0.280	7.5×10^{-6} (0.0000245)	0.759
Extent of total cultivated area of garden (hectares)	1.00*** (0.0000240)	0.000	−0.00004 (0.0000677)	0.605
Number of cultivated Fields (count)	1.08** (0.0250)	0.003	0.04 (0.0529)	0.464
Elevation of residence (masl)	1.00 (0.000106)	0.210	0.0002 (0.000214)	0.259
Elevation range of fields (masl)	0.99 (0.000306)	0.781	−0.0002 (0.000599)	0.760
Multi-species maize field				
No multi-species maize field	.	.	.	.
Multi-species maize field present	0.98 (0.0663)	0.707	0.02 (0.135)	0.898
Self-produced food in diet (calories self-production)	0.52* (0.259)	0.011	−1.03 (0.545)	0.062
Traditional foods in diet (fraction of calories from traditional foods)	1.01** (0.00308)	0.002	0.008 (0.00643)	0.233
Dietary diversity (MDDW)				
MDDW not achieved				
MDDW achieved	0.95 (0.0674)	0.425	−0.08 (0.138)	0.547
Household food security status				
Food insecure (reference)				
Food secure	0.95 (0.0628)	0.455	0.04 (0.129)	0.783
Age (head of household)	1.01*** (0.00209)	0.000	0.01** (0.00447)	0.007
Gender (head of household)				
Male (reference)				
Female	1.14 (0.0742)	0.069	0.04 (0.154)	0.809
Ethnicity and language				
Primary language not Quechua (reference)	.	.	.	.
Primary language Quechua	0.77** (0.0817)	0.002	−0.20 (0.166)	0.225
Household income (soles/year)	1.00*** (0.00000203)	0.000	6.6×10^{-6} (0.00000501)	0.195
Social capital (sum of indicators)	0.99 (0.0128)	0.285	−0.02 (0.0274)	0.373
Geographic sub-area (place)				
Quisqui (reference)				
Amarilis	1.08 (0.0802)	0.361	0.007 (0.163)	0.966
Molinos	1.17* (0.0787)	0.044	0.30 (0.160)	0.066
Level of education (head of household)				
No education (reference)				
Incomplete primary	1.10 (0.0948)	0.293	−0.00005 (0.198)	1.000
Complete primary	0.83 (0.123)	0.140	−0.16 (0.241)	0.499

(Continued)

TABLE 4 | Continued

Factor	Richness incidence rate ratio (standard error)	*P*-value	Shannon Evenness coefficient (standard error)	*P*-value
Incomplete secondary	0.90 (0.125)	0.381	−0.26 (0.254)	0.300
Complete secondary	0.89 (0.138)	0.387	−0.36 (0.276)	0.192
Post-secondary	2.72** (0.289)	0.001	1.32 (0.755)	0.084
Degree of commercialization (agricultural fields)	0.99* (0.000964)	0.047	−0.003 (0.00195)	0.100
Climate and climate change (number adaptations)	1.02 (0.0224)	0.372	0.008 (0.0446)	0.853
Agrobiodiversity loss awareness	1.02 (0.0309)	0.474	0.04 (0.0629)	0.567
Pseudo R^2	0.15			
R^2			0.24	

Values for the model with richness as the dependent variable are incidence rate ratios from Poisson regressions adjusting for the other covariates shown. Values for the model with Shannon Evenness as the dependent variable are partial regression coefficients from OLS regressions adjusting for the other covariates shown. n = 130 for both models. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

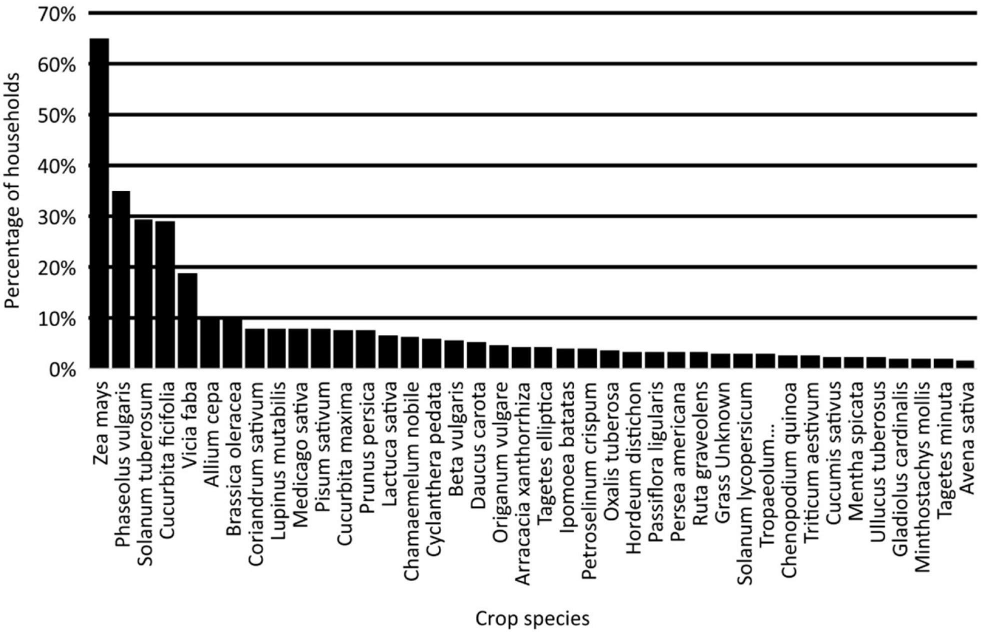

FIGURE 3 | Frequency of cultivated species in crop fields of households ($n = 268$).

Results showed the small extents of total cultivated crop-field and home-garden areas (mean values of 0.361 hectares and 0.0925 hectares, respectively) among sampled households. Similarly, low values were estimated regarding food security (i.e., high food insecurity; 58.7%), income, education, and elevation range (**Table 2**). Estimated household-level capabilities for food production included field numbers (2.5/household), self-produced food in the diet (36.5%), traditional foods in the diet (34.2%), and degree of agricultural commercialization (42.4%) (**Table 2**). These values reflected limited resource access and hybrid traditional-modern food customs including combined non-market/market linkages.

Certain estimated conditions showed large standard deviations. This high variation occurred in legume crop rotations that were defined as leguminous food and forage crops (mean index value 0.60; standard deviation 0.62) and numbers of fields with chemical fertilizer use (mean value 0.64; standard deviation 0.77). Mean climate change adaptations and elements of agrobiodiversity-loss awareness were low-moderate (2.67 and 1.22, respectively). Sample sizes for results estimated in this

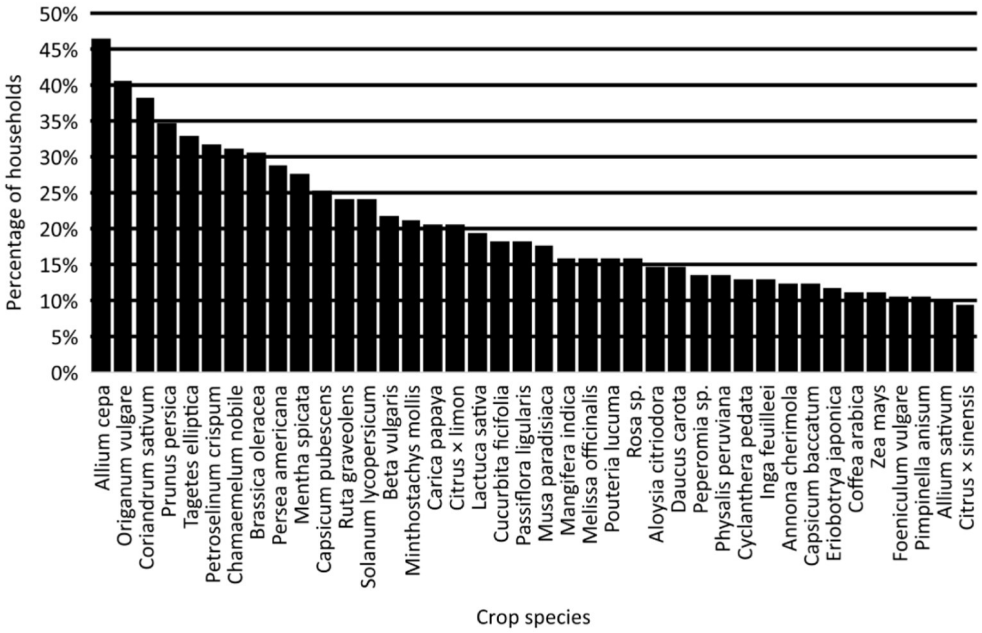

FIGURE 4 | Frequency of agriculturally managed species in home gardens of households (*n* = 159).

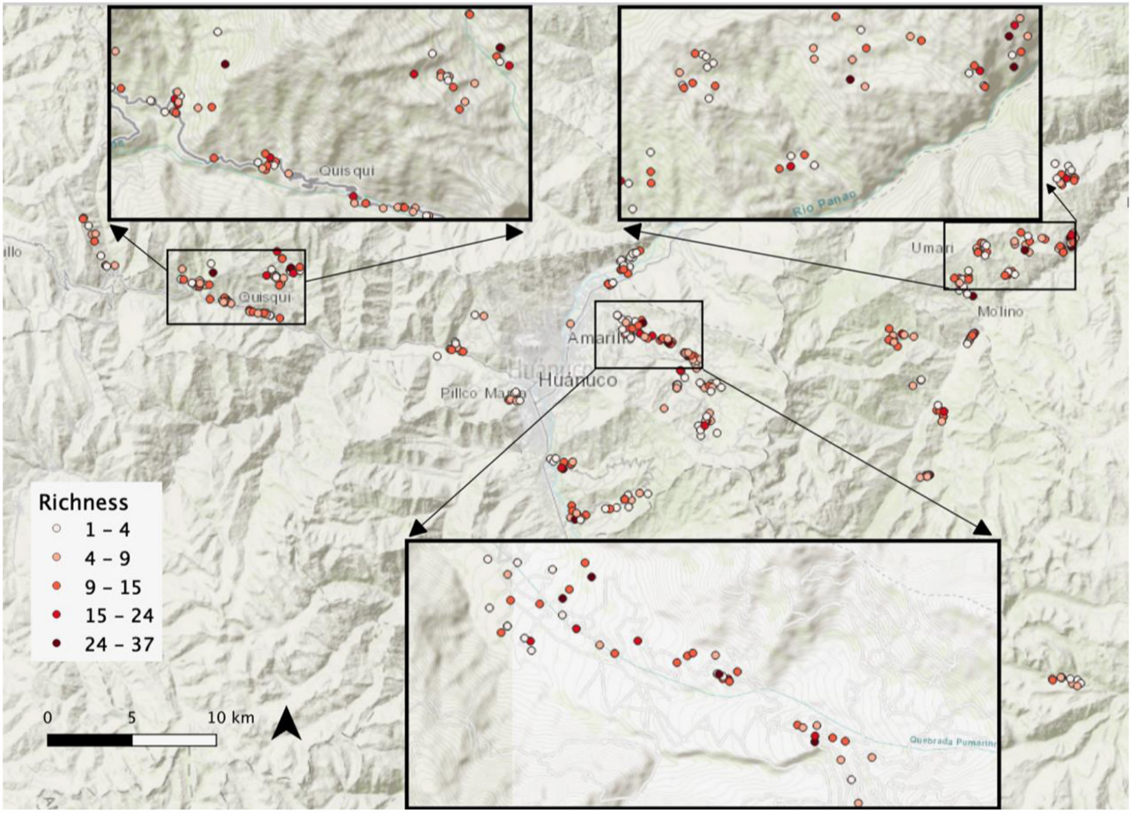

FIGURE 5 | Map of species-level richness of agrobiodiversity (combined richness counts of fields and gardens) among households in Huánuco, Peru.

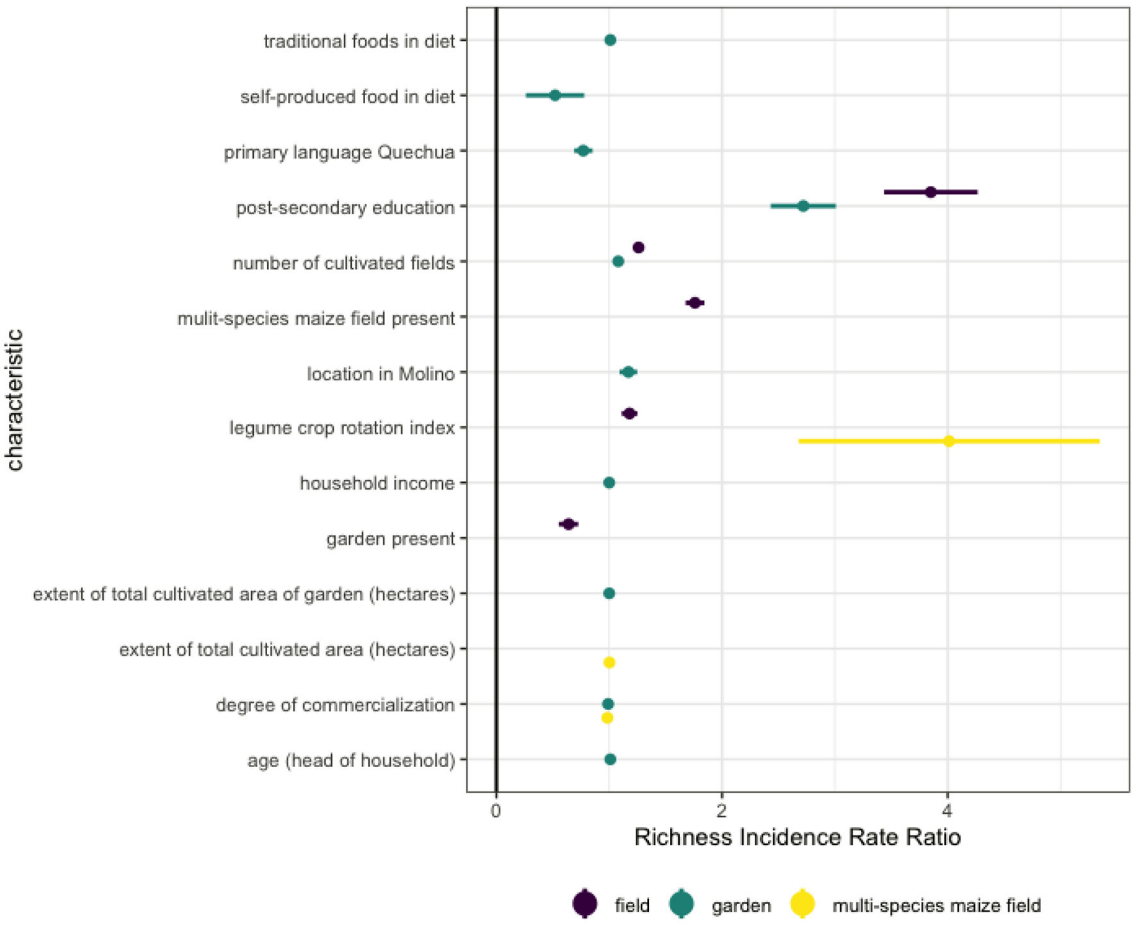

FIGURE 6 | Coefficients and standard errors of significant factors in results of Poisson regression models for richness in agrobiodiversity-and-food spaces (field, garden, multi-species maize fields; each color represents an individual regression model).

paragraph and the preceding varied from 100 to 300 households with most estimates statistically robust. Detailed definitions, data sources, and statistical estimates are given in **Tables 1**, **2**.

Regression Models

Social-ecological and political-ecological factors incorporated in this study's AKF-guided model explained ~16% of variability in the species richness of crop fields (RIRR, Pseudo $R^2 = 0.16$, **Table 3**). These factors accounted for 45% of the variability in the species evenness of these fields (OLS, $R^2 = 0.45$, **Table 3**). In the case of home gardens, social-ecological and political-ecological factors of the AKF-guided model explained ~16% of variability in the species richness of these spaces (RIRR, Pseudo $R^2 = 0.15$, **Table 4**). These factors accounted for 24% of the variability in the species evenness of these fields (OLS, $R^2 = 0.45$, **Table 4**). Social- and political-ecological factors of the AKF-guided models produced similar results to **Tables 3**, **4** using other biodiversity measures as the dependent variables (Materials and Methods; **Supplementary Tables 1, 2**).

Both the species-level richness and evenness of field crops were significantly associated with a set of five factors (**Table 3**). Field number and presence of a multi-species maize field (*maizal*) were most significant in the main model of crop fields ($P < 0.001$; **Table 3**). These highly significant statistical associations occurred across the range of models using the additional agrobiodiversity measures (**Supplementary Tables 1, 2**) as well as the AKF sub-model of farm characteristics (**Supplementary Table 3**).

Field-level richness and Shannon diversity measures showed that legume crop rotation was strongly associated though less significantly ($P < 0.05$; **Table 3**). Additional factors, types of association, and significance levels in the main model of crop fields (**Table 3**) varied among the positive associations of species richness to garden presence ($P < 0.001$) and post-secondary education ($P < 0.01$). Field evenness was negatively associated with the presence of a garden ($P < 0.05$) and the sub-area of the Molinos landscape ($P < 0.05$).

In home gardens, species-level richness was significantly associated with a set of nine factors and the Shannon evenness measure with one (**Table 4**, 2nd and 3rd columns). Age of household head was positively associated at highly significant levels with the species richness ($P < 0.001$) and species evenness of gardens ($P < 0.01$) (**Table 4**). Other factors showing high and positive associations with the species richness of home gardens

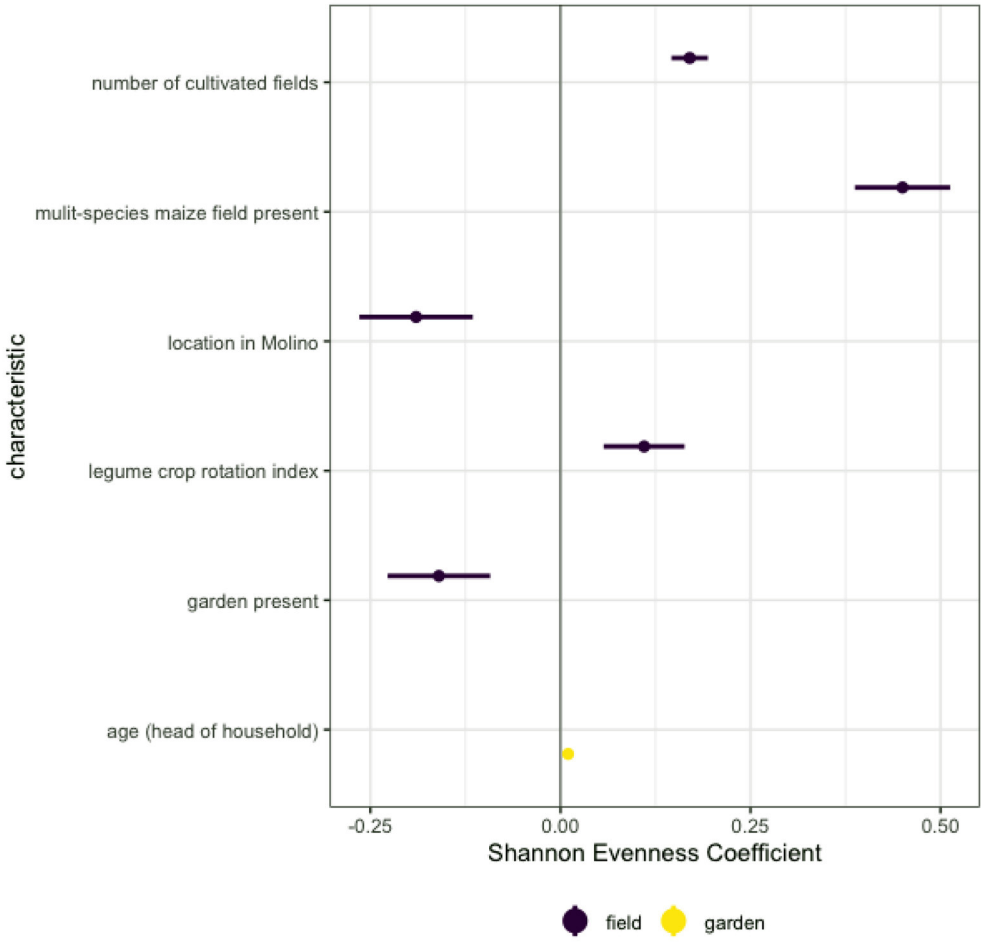

FIGURE 7 | Coefficients and standard errors in regression results on factors in ordinary least squares regression models for Shannon evenness in agrobiodiversity-and-food spaces (field, garden; each color represents an individual regression model).

were garden cultivated area ($P < 0.001$), field number ($P < 0.01$), traditional food in diet ($P < 0.01$), Quechua language ($P < 0.01$), household income ($P < 0.001$), and extent of post-secondary education ($P < 0.01$). Additional factors showed significant positive associations albeit at lower statistical levels. These included the sub-area of the Molinos landscape ($P < 0.05$) and degree of product commercialization ($P < 0.05$).

Individual social- and political-ecological factors identified as statistically significant represented each the four AKF themes (**Figures 6**, **7**) and offered comparisons to previous agrobiodiversity models (last column of **Table 1**) as detailed in the Discussion.

Agroecological and Livelihood Characterization of Keystone Spaces

Agroecological and livelihood characteristics were compared among keystone agrobiodiversity-and-food spaces comprised of multi-species maize fields, other crop-field types, and home gardens. Identification of multi-species maize fields (*maizales*) as an additional keystone space was based on above regression results and fieldwork information (**Figure 8**), including conversations with local people explaining importance. Following above results, further focused analysis of multi-species maize fields as a key space (**Supplementary Table 11** and **Figure 6**) showed the highly positive effect of legume crop rotation ($P < 0.001$), moderate-high correlation with overall field area ($P < 0.01$), and negative association with agricultural commercialization ($P < 0.01$).

Fallow and crop rotation were moderately and highly common in multi-species maize fields (35.2 and 86.2%, respectively) and other field types (32.7 and 76.1%, respectively) (**Table 5**). By contrast, these two practices were applied at low levels in home gardens (1.6 and 4.9%, respectively) (**Table 5**). Intercropped polycultures (planting areas with more than one food species), crop rotation, and legume crops occurred more commonly multi-species maize fields than in other fields. Multi-species mixtures were also moderately common in other crop fields (48.3%). Plant groups with distinct functional roles and traits—legume food and forage crops; the suite of trees, shrubs, and perennials managed in cultivation; and maize—occurred at different levels in the three key agrobiodiversity-and-food spaces (**Table 5**).

FIGURE 8 | Multi-species maize field (maizal) functioning as "key agrobiodiversity-and-food space" in fieldwork visit (February 2017). Photo credit: Karl Zimmerer.

Estimation of the frequency of legume crops and edible managed plants was distinctive among multi-species maize fields, crop fields, and home gardens (71.4, 37.1, 34.6%, respectively; **Table 5**). Leguminous taxa provisioning important foods in the sample consisted of Phaseolus vulgaris (*frijol*, *vainita*, or *numia*), Inga feuilleei (*pacay*), Caesalpinia spinosa (*tara*), Pisum sativum (*arveja*), Vicia faba (*haba*), Lupinus mutabilis (*tarwi*), Arachis hypogaea (*mani*), Inga edulis (*guaba*), Lens culinaris (*lenteja*), and (Medicago sativa *alfalfa*; important as an animal food) as well the widespread ground-covering clover Trifolium spp. (*trebol*). A total of 51 tree species were managed and cultivated, as well as 20 species of perennial herbs.[1]

Estimated relative levels of dietary and income importance varied substantially among the key agrobiodiversity-and-food spaces (**Table 5**). Multi-species maize fields (*maizales*) typically rated intermediate between crop fields (highest levels) and gardens (lower levels yet still important to diet).

DISCUSSION

The Agrobiodiversity Knowledge Framework (AKF) and Comparative Model Results

This study's use of the interdisciplinary Agrobiodiversity Knowledge Framework (AKF) generates reflection on and comparisons with other SDG 2-relevant research. Overall, the AKF framework was thematically comprehensive, theoretically cohesive, and methodologically innovative in predicting agrobiodiversity that is linked to SDG 2-related nutrition security in our overarching design that integrates the agrobiodiversity analysis here with focus on food, nutrition, and diet research (**Figure 1B**; Jones et al., 2018; Zimmerer et al., 2020).

Results showed significant associations across each of the four main themes of AKF predictive factors (**Figure 1A**; agroecology-food/nutrition-governance including sociocultural factors-global change impacts) that provide insights to address SDG 2. First, the AKF-guided models offer a demonstration of agroecological factors (e.g., legume crop rotation; **Table 3**) positively linked to agrobiodiversity. This linkage combines with results on the importance of leguminous food crops to nutrition wellbeing (Jones et al., 2018). Farm-level, resource-access factors were similarly important. For example, access to a garden both determined agrobiodiversity outcomes as shown in this study while it was also associated with favorable nutrition outcomes (Jones et al., 2018). This study's AKF-guided demonstration of well-proven linkages to nutrition build on initial calls (Jarvis et al., 2007; Hajjar et al., 2008) to provide concrete evidence of agrobiodiversity functions that can address SDG 2.

Second, the AKF shows that food and nutrition can operate as significant predictors (**Table 4** and **Supplementary Table 8**). This AKF result is novel since the predominant view is to treat nutrition, food, and other SDG 2-related conditions solely as outcome variables. Instead, it highlights influential bi-directional interactions in which food and diet can serve as model inputs to explain agrobiodiversity, We urge this insight be built into SDG 2 approaches.

Third, AKF-guided analysis of governance predictors, including socioeconomic factors, were significant in the results (e.g., income; **Table 4**). Other significant governance factors were sociocultural factors in the changing spatial strategies of food-growing (multi-species maize fields), agrobiodiversity knowledge (Quechua language), and institutional influences (e.g., school-based education; **Tables 3**, **4**). Each of these factors potentially serves as a strong linkage in addressing SDG 2, including other governance factors (such as the potential major influence of seed systems Arce et al., 2019a) and public-good policies (Graddy-Lovelace, 2021).

Fourth, results showed AKF-SDG linkages involving global-change factors in the significant association of the number of fields with agrobiodiversity (**Table 3**) since the dispersion of fields provides adaptations to weather variation propelled by climate change. At the same time, the resulting higher level of crop diversity has been shown in our related research to predict favorable nutrition outcomes (Jones et al., 2018).

Comparability of model results is needed to advance the use of agrobiodiversity and agroecology to address SDG 2. The AKF supported a much-needed, cohesive approach to interdisciplinary research to enable rigorous cross-case comparisons and policy dimensions ranging from incentives and capacity-building to new initiative such as participatory varietal selection using agrobiodiversity to address SDG 2 (Scurrah et al., 2019). Here we briefly use AKF-guided results to discuss comparisons with other agrobiodiversity studies relevant to SDG 2 approaches and conclude the section by synopsizing this study's model results.

This study's model results show various similarities when compared to related agrobiodiversity studies holding promise for SDG 2 approaches (e.g., Pseudo $R^2 = 0.1883$ of species-level agrobiodiversity in important research linked to food consumption and security in the Northern Ecuadorian Andes;

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[1] Trees and herbs provided important food and nutrition though the legume crops, as a category, were more important as a source of food and demonstrated determinant of healthy diet and nutrition outcomes among local populations in Huánuco and elsewhere (Jones et al., 2018).

TABLE 5 | Characterization of key farm and food-producing spaces according to livelihood importance and the frequencies of soil and soil-nutrient management (Huánuco, Peru).

Livelihood and agroecological components (2017, unless specified otherwise)	Fields (*chakras*, *parcelas*)[a]	Multi-species maize fields (locally *maizales*)	Gardens (locally *huertos*)
Dietary input to self-produced food (37% of average food consumed; 1.0 = highest; see text for methods)	1.8	2.2	2.4
Income input to farm income (1.0 = highest; see text for methods)	1.6	2.8	4.0
Sample size (numbers of units)	742	196	182
Field fallow (2011–2017)	32.7%	35.2%	1.6%
Crop rotation (2013–2017)	76.1%	86.2%	4.9%
Multi-species fields	48.3%	100.0%	100.0%
Legume food and forage crops	37.1%	71.4%	34.6%
Trees, shrubs, and perennials	15.2%	13.8%	67.0%
Maize	41.4%	100.0%	10.4%

[a] *Does not include multi-species maize fields (maizales).*

Skarbø, 2014, p. 723). In addition, our results found similar factors to be significance (e.g., field number and education level). Comparisons are partly limited, however, since the other research did not model determinants of evenness or garden-specific agrobiodiversity [see also Velásquez-Milla et al. (2011) on Huánuco agrobiodiversity custodian farmers that identifies similar statistically significant factors but does not report model-level results; Skarbø, 2014]. As a result, this study recommends comparisons to thematically related social- and political-ecological modeling of agrobiodiversity evenness, such as species-level agrobiodiversity in coastal Nicaragua ($R^2 = 0.34$; Williams, 2016, p. 234) whose general similarity suggests SDG 2 promise.

Our model-level results on the social- and political-ecological determination of home garden agrobiodiversity in Huánuco suggest extended geographic comparison to SDG 2-relevant research in the neighboring Amazon region (e.g., Ban and Coomes, 2004, p. 353). Individual factors identified as highly significant in this study (e.g., garden area and gardener experience) were similar (Ban and Coomes, 2004, p. 353), though different statistical techniques and lack of model-level estimation and evenness estimates limit further direct comparison.

Finally, this study's results from regression models account for species richness to a similar degree in both crop-field and home-garden analysis (Pseudo R^2 values of 0.16 and 0.15, respectively) while evenness, as measured by the Shannon diversity index, differs substantially among crop fields ($R^2 = 0.45$) and home gardens ($R^2 = 0.24$). Relative species abundance in home gardens is known to vary depending on the complex characteristics of individual households (Ban and Coomes, 2004; Coomes and Ban, 2004; Wezel and Ohl, 2005; Perrault-Archambault and Coomes, 2008; Whitney et al., 2018), which may contribute to the lower results of the evenness model.

Biodiversity Estimations and the Social- and Political-Ecological Factors

This study's estimations of agrobiodiversity levels and specific social- and political-ecological factors offer valuable specific comparisons to SDG 2-related research as well as general research advances. Our result on the species-level richness of crop fields (mean 3.7 species/household) was similar though less than findings in the Ecuadorian Andes (7.22 species/household; Skarbø, 2014, p. 714) whose fields traversed a significantly larger elevation gradient (1,000 meters). This study's results on specifies-level richness of home gardens (mean 10.2 species/household) resembled the richness of cultivated species of fruits, vegetables, and herbs (10.2 species/household) that were grown the Ecuadorian Andes (Skarbø, 2014, p. 714). Furthermore, this study's results on total agrobiodiversity species richness in Huánuco, when summed across the households' crop fields and home gardens, resembled an additional study of the Ecuadorian Andes (Oyarzun et al., 2013, p. 525).

Another useful comparison is to local high-agrobiodiversity custodian farmers in Huánuco (Velásquez-Milla et al., 2011) and high-level agrobiodiversity hotspots elsewhere in the Peruvian Andes (Arce et al., 2019a). The current study complements these others, while our sample design and methods were distinct since we integrated focus on agrobiodiversity's roles in SDG-related diets and nutrition that included the randomized sampling of households (see also Jones et al., 2018; Zimmerer et al., 2020).

Important to highlight as a research advance is this study's demonstration that combined biodiversity richness and evenness estimates are needed to understand agrobiodiversity's nexus role connecting to both food-nutrition, such as SDG 2, and agroecology.

Finally, individual factors determined to be significantly associated with agrobiodiversity in this study (see previous sub-section) conform hypotheses in **Table 1** and need to information expanding SDG 2 research globally. Overcoming barriers to link or couple agrobiodiversity access and related SDG 2 benefits for food sovereignty (Zimmerer et al., 2020) will require promoting agroecological management, garden cultivation, and livelihood improvement in addition to income and education as parts of the agendas of social justice and food and nutrition security.

Select factors not showing statistical significance in this study's model results, such as field size and elevation range (**Tables 3**, **4**), help to explain contextual influences. Extremely limited size of cultivated areas in this study (0.404 hectares/household; **Table 2**) is typical of many places in the Andes (e.g., 0.5-hectare farms are common in the central highlands of Ecuador; Oyarzun et al., 2013, p. 523) and smallholder farming globally (van Vliet et al., 2015). Likewise, this study's result on the limited elevation range among fields (**Table 2**) did not result in a significant model result though it is consistent with fieldwork observations of the clustering of small-size fields and gardens near residences. Additionally, this study's findings showed the high frequency of global change factors among surveyed households (e.g., climate change adjustments and elements of agrobiodiversity-loss awareness; **Table 2**), though this study's regression results did not reveal specific statistical associations to these variables.

A Keystone Agrobiodiversity-and-Food Space: Multi-Species Maize Fields

This study's focus on new descriptive, statistical, and conceptual understandings of the role of multi-species maize fields (*maizales*) as a Keystone agrobiodiversity-and-food space is designed to offer a novel contribution and to build on previously hypothesized functions (see multi-species maize fields, **Table 1**). Model results demonstrate that multi-species maize fields, which are distinct due to the types and extent of intercropping (see Results, Agroecological and Livelihood Characterization of Key Spaces), hold a high level of significance in agrobiodiversity relationships (**Tables 3**, **4**). Multi-species maize fields comprise a key space of broad significance to the nexus of agrobiodiversity-agroecology-SDG 2.

We propose the concept of "Keystone agrobiodiversity-and-food space" to describe multi-species maize fields (*maizales*) owing to multi-faceted functions. These fields of Huánuco incorporate widespread inter-plantings of Andean common beans (*frejol*, Phaseolus vulgaris), Andean squash (most commonly *zapallo*, Cucurbita maxima), and *arracacha* (giant Andean carrot or parsnip, Aracacia xanthorrhiza), among other species. Agrobiodiverse *maizal* assemblages, which are extensive in western South America, are distinct while partly resembling the well-known *milpa* system of Mexico and Central America that is agrobiodiverse and nutritionally important (Toledo and Barrera-Bassols, 2017; Novotny et al., 2021).

Notable nutrient management techniques characterize the agroecological functions of the multi-species maize field as a "keystone agrobiodiversity-and-food space" with extensive rotation of crops (86.2% of *maizales* incorporate crop rotation; **Table 5**). Various agrobiodiverse species depend on seed flows and rotated planting sites that link the *maizal* system to other fields. For example, Huánuco households undertaking the non-*maizal* field cropping of Andean maize, Andean common beans and Andean squash species frequently depend on *maizal*-based seed sources and rotated planting sites, and vice versa. A second major function is continued utilization and development of agrobiodiversity management knowledge. This role is crucial since cultivated area and field number are extremely limited among Huánuco households (**Table 2**). In this context, the multi-species maize field (*maizal*) enables the crucial continuation of knowledge and practices of production as well as food processing and consumption that are vital to agrobiodiversity-SDG 2 linkages.

Another key agrobiodiversity-support function of the Andean multi-species maize field is the concentration of livestock grazing on above-ground plant residues following harvest. This emphasis is crucial to the functioning of ecological nutrient management of agrobiodiversity-containing *maizales* as well as nearby fields. Home gardens (locally *huertos*), which are distinct from multi-species maize fields, are also "keystone agrobiodiversity-and-food spaces" though they contain lesser degrees of the linkage functions described above.

Concepts and Barriers for "keystone Agrobiodiversity-and-Food Spaces"

This study's concept of "keystone agrobiodiversity-and-food spaces" is supported by advances in ecological theory extending the keystone species idea from an original food-web focus to other connectivity (e.g., Davic, 2003). An analogous development has occurred in the concept of "cultural keystone species" (Coe and Gaoue, 2020) being expanded to agroecological applications (Nabhan, 2018; Zapico et al., 2020). Use of "keystone" here signifies that addition or loss leads to major changes in occurrence or abundance of other species.

The "keystone agrobiodiversity-and-food spaces" concept is designed to rework the single-taxon definition of a keystone species to one centered on the vital and distinct roles of spatially, culturally, and agroecologically distinct suites of interacting species. Spatial dynamics and influence of food-generating units is traditional in farming and land use (Brookfield, 2001; Mayer, 2018). Changing spatial dynamics of agrobiodiversity pose new challenges and opportunities regarding agroecological sustainability (De Molina et al., 2019). Supporting the positive factors enabling multi-species maize fields (**Supplementary Table 11** and **Figure 6**), such as legume crop rotation, will need to overcome access barriers (e.g., currently multi-species maize fields are linked to larger, less resource-poor farms among indigenous Huánuco smallholders; **Supplementary Table 11**; Zimmerer et al., 2020).

In sum, the multi-species fields or *maizales* of Huánuco function as a distinct, locally recognized, and valued agrobiodiversity-and-food space with widespread intercropping, associated agrobiodiversity, and nutrient management. The latter's characterization (**Table 5**) is preliminary in scope and is intended to stimulate research. We anticipate other "keystone agrobiodiversity-and-food spaces" to include the multi-species, high-agrobiodiversity fields of Andean tuber crops in sectoral fallow management (also known as common field agriculture; Arce et al., 2019b; Vanek et al., 2020). *Milpa* agriculture of Mexico and Central America is another vital space occurring in highly dynamic contexts (Tamariz, 2022) with key linkages and agroecological functions of agrobiodiversity anticipated to be changing rapidly.

Further Links to Future Research

Finally, this study suggests future research avenues centered on AKF-guided approaches to addressing SDG 2 through agrobiodiversity models integrating one or more emphases of agroecology, biodiversity science, and comparisons with existing studies. It indicates the promising role of "keystone agrobiodiversity-and-food spaces" well-suited to expanded integration with these areas of emphasis. Further new research is needed on functional diversity and multi-functionality in agroecology (Blesh, 2018) suited to SDG 2 goals. New AKF-guided modeling approaches related to SDG 2 goals could involve alternative sampling and statistical methods such as Principal Components Analysis, path analysis, constrained ordination, permanova, systems modeling, and reduced-variable parsimonious models.

CONCLUSION

Modeling of social- and political-ecological factors using the interdisciplinary Agrobiodiversity Knowledge Framework (AKF, **Figure 1A**, **Table 1**) was combined with nutrient management characterization of keystone agrobiodiversity-and-food spaces that linked to our project on improving nutrition, diets, and SDG 2 (Zero Hunger). Focused on a continued case study in Huánuco, Peru, the AKF guided the selection, design, analysis, and interpretation of determinants of agrobiodiversity. The latter was estimated using the biodiversity statistics of species-level richness and Shannon diversity index (as well as five additional biodiversity indices) applied both to crop fields and home gardens.

Model results showed significant associations of the farm and agroecological characteristics of field number, garden area, and legume crop rotation. Other factors identified as significant in agrobiodiversity modeling corresponded to the AKF categories of diet and nutrition; social/socioeconomic and cultural factors (governance); and global change. The AKF model was shown to be thematically comprehensive, conceptually cohesive, and timely in focusing on agrobiodiversity-SDG 2 synergies and communicating new research on dynamic, change-prone agrobiodiversity interactions that are increasingly influential (Zimmerer, 2010; Dwivedi et al., 2013; Baumann, 2022; Tamariz, 2022; Tamariz and Baumann, 2022; Zimmerer et al., 2022).

The study's design enabled comparison to other models and estimation that is crucial to advancing agrobiodiversity knowledge, policy, and initiatives to promote SDG 2. Effectively integrating AKF-guided agrobiodiversity modeling and estimation with SDG 2 research relied on incorporating characterization of ecological nutrient management using the concept of "key agrobiodiversity-and-food spaces." Characterization focused on soil- and plant-based elements of nutrient management, with results demonstrating the extensive utilization of field fallow, crop rotation, multi-species fields, legume crops, and managed plantings of trees, shrubs, and perennials as well as maize.

The concept of "keystone agrobiodiversity-and-food spaces" is proposed and developed to account for the combined prevalence and functions of crop fields, home gardens, and multi-species maize fields (*maizales*) in the changing agri-food systems of indigenous smallholders in Peru. Results demonstrated the strong agrobiodiversity associations and ecological nutrient management of each key space with focus on multi-species maize fields. As a key agrobiodiversity-and-food space, the multi-species maize fields are beneficially linked to agrobiodiversity, ecological nutrient management, and food and market capacities, thus offering vital contributions to SDG 2.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

The studies involving human participants were reviewed and approved by Instituto de Investigacion Nutricional, Lima, Peru. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

AUTHOR CONTRIBUTIONS

KZ: conceptualization and writing—original draft. HC-K, SH, AJ, KZ, and FP: methodology and supervision. HC-K, SH, AJ, KZ, FP, and MT: investigation. KZ, AJ, SH, RT, CH, and KN: data and analysis. KZ, SH, AJ, and HC-K: writing—review and editing and funding acquisition. RT and CH: visualization. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.734943/full#supplementary-material

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Legume Cover Crop Contributions to Ecological Nutrient Management in Upper Midwest Vegetable Systems

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Cover cropping, especially with legumes, is a critical approach to ecological soil nutrient management as a means to meet Sustainable Development Goal (SDG) 2, addressing food security issues via sustainable agriculture approaches. However, cover cropping in some of the most intensified food production regions of the northern U.S. is challenged by short growing seasons and harsh winters with variable temperatures and increasingly erratic snowfall. In this study, we explore the potential of winter annual legume cover crops to augment soil organic carbon (C) and nitrogen (N) stocks within a horticultural cropping system under climate conditions that allow only modest cover crop biomass production. We compared hairy vetch, cereal rye, red clover, and a hairy vetch/rye biculture in a randomized complete block design at two sites (North Central and Southwest Research and Outreach Centers in Minnesota) over 2 years. Cover crops were established in fall and terminated in spring prior to sweet corn planting, and soils sampled both at pre-cover crop termination and 2 weeks post-termination. We determined several indicators of C and N dynamics, including microbial biomass C (MBC), permanganate-oxidizable C (POXC), particulate organic matter C and N (POMC and POMN, respectively), extractable soil N (EXTN), and potentially mineralizable N (PMN). Out of all treatments evaluated, vetch production increased soil EXTN the greatest after 2 weeks, contributing two to 11 times more EXTN to soils compared to non-vetch treatments, meeting N requirements for sweet corn in three out of four site-years. Overall, time of sampling, either pre-or post-termination, consistently impacted soil measurements, with $p < 0.05$ in 20 out of 24 soil parameter × site-year combinations. Study results suggest that cover crops planted in colder northern climates during winter fallow periods can supply valuable N following spring termination, but termination effects on labile C and N pools are mixed. Our findings advance understanding of how cover cropping can support SDG 2 outcomes by assessing cover crop legume systems under biophysical conditions that challenge cover crop integration in agroecosystems.

Keywords: cover crops, legumes, nutrient cycling, organic cropping systems, soil organic matter

INTRODUCTION

The Sustainable Development Goal (SDG) 2 calls for improved understanding of sustainable and ecological agriculture approaches that meet both sustainability and food production goals. With fewer than 10 years remaining to mobilize resources and take action, the time to pay targeted attention to localized solutions that result in increased reliance on ecological processes for food production is now. Integration of legume cover crops as "green manures" into annual cropping systems, especially those producing horticultural crops for human consumption, is of increasing global interest due to their potential to provide ecologically-sourced nitrogen (N) to crops, as well as improve long-term soil sustainability via contributions of organic matter (Robačer et al., 2016; Brennan, 2017; Seman-Varner et al., 2017; Wauters et al., 2021). In humid continental climates, which make up a large portion of global cropland, cover crops could serve to improve food security via targeted ecological management of soil nutrients by utilizing the typically fallow winter months for cover crop establishment and production.

Humid continental northern climates are a prime target for ecological nutrient management because high crop production potentials and demands have resulted in prevalence of monoculture, conversion of grassland to cropland, and high fertility inputs. These combined factors, in addition to a changing climate, have contributed to nutrient decoupling and resulting nutrient losses from these soils (Zhang et al., 2021). However, these northern climates present unique barriers to integrating winter annual cover crops in crop rotations. Summer crop planting windows are relatively short, and maximization of crop production during these periods means that there are frequently few growing degree days (GDD) available for fall cover crop establishment and spring maturation (Hively and Cox, 2001; Teasdale et al., 2004). Cover crop implementation is also limited by extreme minimum winter temperatures and variable snow cover (Larsen et al., 1987), which can threaten winter survival of many common cover crop species that thrive in warmer climates. These challenges limit general cover crop success and derived benefits, as winter cover crops must first establish successfully in the fall in order to promote winter survival, and most soil gains result from ample root and shoot biomass production (Puget and Drinkwater, 2001; Finney et al., 2016). Cooler regions would benefit from a wider range of cover crop options, especially those that include legumes.

While winter cover crop integration into row cropping systems is well studied, vegetable systems are less understood, and may offer unique opportunities for winter annual cover crops in these northern climates because of the shorter growing season required by some vegetables as compared to row crops (Dabney et al., 2001). Cover crop adoption in northern region vegetable systems is a relatively recent phenomenon. Since certified organic vegetable farmers are required to both build soils and diversify rotations, and since they rely on ecologically-based fertility inputs over synthetic ones, these farmers have been early adopters of cover crops as a tool for ecological soil management. A survey of 152 organic vegetable farmers in Wisconsin showed cover crop adoption has increased dramatically from <20% of farmers in the 1980s to 92% in 2013, with most adoption occurring after 2005 (Moore et al., 2016). The primary driver encouraging cover crop use by these adopters was perceived soil benefit, including increases in soil fertility, soil organic matter, and structure.

Diversification with winter annual legume cover crops may be easier with shorter-duration warm season vegetable crops, such as zucchini or cucumbers, than longer-duration ones, such as sweet corn or tomatoes, since crops that mature earlier in the fall leave more time for cover crop establishment prior to winter. Rotation of winter annual cover crops with longer-duration warm season summer vegetables may be more difficult, as longer crops leave less time for cover crop establishment. This, combined with early spring termination to accommodate cool season vegetable crop planting, means that nutrient benefits from winter cover crops may not be achieved due to resulting reduced growing degree days and biomass production (Mirsky et al., 2017). Sweet corn is a major horticultural crop in the Upper Midwest (*FarmProgress*, 2018), and its higher days to maturity (75–90 days) relative to other warm season vegetables make it a good model for evaluation of cover crop rotations in longer-duration warm season crops in cool climates. The viability of these strategies and the potential for legumes to supply significant N to subsequent horticultural crops under highly restrictive climatic conditions remains largely unknown.

Legumes are valuable for their capacity to fix atmospheric N and improve soils' long-term N cycling activity and organic matter accrual (Marriott and Wander, 2006; Lynch, 2015). Cover crop N contributions are a function of shoot and root biomass production, yet since legume cover crop inclusion in northern climate cropping systems can be restricted by establishment constraints, poor winter survival (Hively and Cox, 2001), and limited winter-hardy varieties (Wilson, 2007; Silva, 2014), these benefits are commonly not achieved. Poorly performing legume cover crops can limit both aboveground and belowground biomass contributions, reducing potential benefits from these crops via N fixation and soil N uptake. Net N mineralization from cover crop decomposition is dependent on residue quantity, quality, incorporation method, as well as soil moisture and temperature, with legume residues known to mineralize more rapidly than those of grasses (O'Connell et al., 2015). While C/N ratios vary depending on maturity and species, spring-terminated legumes in the Upper Midwest can be as low as 10:1 (Lawson et al., 2015), which encourages rapid mineralization prior to cash crop planting. In fact, an analysis of legume cover crop monocultures and bicultures across nine farms in southeastern Michigan showed an increase in C and N mineralization after 2 years relative to the no cover crop control, as well as other labile SOM parameters such as free particulate organic matter (POM) and protected POM (Blesh, 2019). Less is known about even shorter-term effects (∼weeks to months) of cover crop residue incorporation on labile nutrient parameters such as permanganate-oxidizable carbon (POXC), particulate organic matter (POM) carbon (C) and N, microbial biomass C, and potentially mineralizable N (PMN), especially in horticultural systems. This time frame is of interest due to these pools' potential to provide nutrients to a cash crop immediately following a cover crop. Together with bioavailable N, these

TABLE 1 | Soil characteristics of the two experimental sites.

Location	Soil type	Cropping history	pH	CEC (meq)	Bray P (ppm)	Olsen P (ppm)	K (ppm)	% OM
Grand rapids (PER)	Coarse-loamy, mixed, superactive, Haplic Glossudalfs	Transitional land from long-term apple orchard with perennial grasses	5.9	5.9	NA	23	58	2.8
Lamberton (ANN)	Coarse-loamy, mixed, superactive, mesic Typic Hapludolls	25+ year organic cropping history, grain/alfalfa rotation	6.6	NA	10	6	109	4.3

parameters may provide a higher resolution of nutrient coupling dynamics in systems relying on ecological nutrient management.

Understanding the dynamics between cover crop biomass characteristics and soil nutrient cycling processes is a key step to achieve sustainable agroecosystem nutrient management in cooler regions. Our goal was to explore the extent to which winter annual cover crops influence short-term soil C and N cycling dynamics to realize benefits in cold regions with narrow biomass accumulation windows. Previous studies have evaluated winter annual cover crop biomass accumulation in the Upper Midwest (Silva, 2014; Appelgate et al., 2017; Noland et al., 2018; Perrone et al., 2020), cover crop influences on labile soil C and N pools (Drinkwater et al., 1998; Puget and Drinkwater, 2001; Bair et al., 2008), and crop dynamics following cover crop termination (Griffin et al., 2000; Leavitt et al., 2011). Our objective was to evaluate short-term (~2 weeks) impacts of cover crop biomass incorporation in a horticultural system on key indicators of soil C and N cycling over the period of initial cover crop decomposition after cover crops are terminated. We evaluated hairy vetch (*Vicia villosa* Roth), cereal rye (*Secale cereale* L.), red clover (*Trifolium pratense* L.), and a hairy vetch/rye biculture compared to a fallow control in a sweet corn production system at University of Minnesota research and outreach centers in southwestern and north-central Minnesota. These sites were chosen because of their contrasting soils and site histories, since legacy effects of management may impact soils' responses to inputs (Tardy et al., 2015; Ontivero et al., 2020; Hermans et al., 2021). We hypothesized that despite relatively short cover crop establishment and maturation periods, legume and rye treatments would both impact soil nutrient cycling dynamics following spring termination and would differ in their effects on soil nutrient responses because of differences in biomass amount and biochemical properties of residues.

MATERIALS AND METHODS

Site Descriptions

The experiment was conducted from September 2015 through August 2017 at two University of Minnesota experiment stations, the North Central Research and Outreach Center, Grand Rapids, MN (LAT: 47.243347, LONG:−93.492622) and the Southwest Research and Outreach Center, Lamberton, MN (LAT: 44.239366, LONG:−95.309855). Grand Rapids is in USDA-designated plant hardiness zone 3b, and Lamberton is in zone 4b. At both locations, fall 2016 was unseasonably wet (see **Supplementary Material**). Lamberton received above average spring rainfall in both years, and Grand Rapids was unseasonably dry during July 2016. Snow cover was generally above 10 cm between January 1 and April 1, although this differed across site and year (See **Supplementary Material**). Soils at the two locations differ widely (**Table 1**, adapted from Perrone et al., 2020). For example, Grand Rapids soil was an Alfisol with 2.8% SOM while Lamberton soil was a Mollisol with 4.3% SOM.

Lamberton experimental fields had an oat (*Avena sativa*) cover crop preceding experimental cover crop seeding in fall 2015 and 2016 with a 25+ year history of organic management. In contrast, Grand Rapids experimental fields, also certified organic, had been converted from long-term rhizomatous quackgrass (*Agropyron repens*) and other perennial grasses to annual production the year prior to the experiment and were cover cropped with winter wheat (*Triticum aestivum* L.) prior to beginning the experiment in fall 2015. In 2016, the preceding crop at Grand Rapids was cereal rye. These two locations had contrasting soil characteristics and management histories; therefore, we refer to the Lamberton site as annual cropping history (ANN) and the Grand Rapids site as unmanaged perennial history (PER) to highlight these differences.

Experimental Design

The experiment was a randomized complete block design replicated across 4 blocks over 2 years, 2015–2016 (Y1) and 2016–2017 (Y2). Separate fields were used at both sites in both years and were characterized as four separate site by year combinations (ANN Y1, PER Y1, ANN Y2, PER Y2). Cover crop species rye (*Secale cereale* L., RYE, Johnny's Seeds, Winslow, ME), medium red clover (*Trifolium pratense* L., CLO, Johnny's Seeds, Winslow, ME), hairy vetch ecotype 1 (*Vicia villosa* Roth, variety-not-stated, Albert Lea Seed, Albert Lea, MN), hairy vetch ecotype 2 (*Vicia villosa* Roth, variety-not-stated, Buckwheat Growers, Wadena, MN), and a rye/hairy vetch ecotype 2 biculture (MIX) were planted at the two research stations in September 2015. For analyses, vetch ecotypes 1 and 2 were combined (abbr. VET) as they were unable to be differentiated at the level of variety. Due to space limitations, vetch ecotype 1 was eliminated from

TABLE 2 | Dates of key field operations for all environments.

	Y1		Y2	
Operation	**PER**	**ANN**	**PER**	**ANN**
Cover crop planting	August 21, 2015	September 1, 2015	August 25, 2016	September 2, 2016
Cover crop biomass sampling	June 5, 2016	May 23, 2016	May 22, 2017	May 25, 2017
Pre-termination soil sampling	June 6, 2016	May 23, 2016	May 22, 2017	May 25, 2017
Cover crop termination	June 6, 2016	May 24, 2016	May 24, 2017	May 26, 2017
Cover crop incorporation	June 6, 2016	May 27, 2016	May 31, 2017	May 30, 2017
Post-termination soil sampling	June 21, 2016	June 7, 2016	June 9, 2017	June 7, 2017

PER Y2 experimental plots but included at ANN Y2. A bare-ground control (NOCC) was also included at both sites in both years. A pre-study trial eliminated Austrian winter pea as a legume treatment in this study due to complete winter kill at both locations. Plots were 3 × 7.6 m, and blocks were separated by 3 m buffers kept free of weeds.

Cover Crop Management

Seeding rates followed recommended rates for organic production (SARE., 2007). Vetch was planted at 28.0 kg ha^{-1}, clover at 13.5 kg ha^{-1}, rye at 117.7 kg ha^{-1}, and the mix contained 28.0 kg ha^{-1} of vetch and 84.1 kg ha^{-1} of rye. Planting depth was 1.25 cm for clover and 2.50 cm for hairy vetch and rye treatments. Cover crop planting occurred in the last week of August or first week of September (for specific dates, see **Table 2**, adapted from Perrone et al., 2020). A 6-row Jang seeder (Mechanical Transplanter, Holland, MI) was used to plant covers at PER Y1 and Y2 and a five-foot wide Marliss drill (Remlinger Manufacturing Company, Kalida, OH) was used at ANN Y1 and Y2.

Cover crops were terminated in late May or first week of June (**Table 2**) and growth stages recorded according to the BBCH-scale, a uniform coding of phenologically similar growth stages of all mono- and dicotyledonous plant species (Meier, 2001). Rye had reached or surpassed 55 in the BBCH-scale (50% heading) at both locations in Y1 but only achieved 37–41 in the BBCH-scale (stem elongation and early booting stage) at PER Y2 and early heading in ANN Y2. At that phenology, percentage of vetch flowering was 601 in the BBCH-scale (5–15%), matching cover crop development and termination of similar studies (Leavitt et al., 2011). Optimal maturity for maximum N accumulation at termination in vetch occurs at ∼605 in the BBCH-scale (50% flowering; SARE., 2007), and 65 in the BBCH-scale for rye (anthesis) is commonly used as a termination point in roller crimping and reduced tillage cover cropping systems (Mirsky et al., 2011). In our study, cover crops were terminated prior to optimal maturity to provide an adequate growing season for sweet corn.

Cover crops were terminated using a John Deere Z950 mower (Deere & Co., Moline, IL) in PER Y1 and Y2 and a Loftness 90M flail mower (Loftness Manufacturing, Hector, MN) in ANN Y1 and Y2. Mower height was set to maximum height (14 cm). Both sites were tilled within 1 week of cover crop termination. Plots in ANN Y1 and Y2 were tilled using a JD 236 tandem folding disk (Deere & Co., Moline, IL) and plots in PER Y1 and Y2 were rototilled with a King Kutter TG-60 YK rototiller (King Kutter, Winfield, AL). In both locations, secondary bed preparation occurred prior to sweet corn planting. In ANN Y1 and Y2, several passes were made with a Kuhn HK 3004D rotary power harrow (Kuhn North America Inc., Brodhead, WI), and several additional rototiller passes were made in PER Y1 and Y2.

Cover Crop Biomass and Soil Sampling

Cover crop and weed biomass were sampled immediately prior to cover crop termination (**Table 2**), pooling four randomly cut 0.1 m^2 quadrats per plot (Wiegert, 1962). Biomass was dried at 60°C for 72 h. After determining dry weight, samples were ground and passed through a 2 mm sieve and then pulverized using a 2010 Geno/Grinder ball grinder (SPEX SamplePrep, Metuchen, NJ) using 5 mm stainless steel ball bearing balls (Craig Ball Sales, Seaford, DE) for 3–10 min at 1,500 rpm.

Soil samples to 15 cm depth were collected immediately prior to cover crop termination as a baseline and ∼2 weeks following termination. These time points were chosen to assess the contribution of cover crop biomass to labile C and N parameters immediately prior to cash crop planting so that the in-season nutrient transfer potential as a result of cover crop biomass incorporation could be evaluated. In each plot, 8–12 2.5-cm diameter cores were collected randomly after removing surface residue, composited, and mixed until homogenous. Fresh soils were immediately placed into coolers after sampling and temperature was maintained at 4°C until conducting analyses within 7 days. Samples for dry analyses were dried at 35°C for 48 h and then ground to 2 mm. Soil moisture was determined gravimetrically.

Soil Analyses

Permanganate-Oxidizable Carbon

Permanganate oxidizable carbon (POXC) is a fraction of active C, chemically defined by the quantity of potassium permanganate reduced in reaction with a quantity of soil (Weil et al., 2003). POXC was performed based on methods outlined by Culman et al. (2012). Briefly, 20 mL 0.02 M $KMnO_4$ was added to 2.5 g soil, shaken for 2 min, and settled for 10 min. Absorbance of the resulting supernatant was determined on a 300 µL subsample using a spectrophotometer at 550 nm and averages were taken across the three replicates and converted to mg kg^{-1} soil using the following equation:

$$POXC\left(mg\,kg^{-1}\,soil\right) = \left[0.02\,M\,KMnO_4 - \left(a + b\,x\,Abs\right)\right] \times \left(9,000\,mg\,C\,mol^{-1}\right) \times \left(\frac{0.02\,L\,KMnO_4}{x\,kg\,soil}\right)$$

where 0.02 M $KMnO_4$ is the concentration of the starting solution; *a* and *b* are the intercept and slope of the standard curve, respectively; *Abs* is the absorption of the sample; 9,000 mg is the quantity of C oxidized by 1 mol $KMnO_4$; 0.02 L is the volume of $KMnO_4$ solution reacted; and *x* is the mass of soil (kg) in the reaction.

Particulate Organic Matter Fractionation

Coarse fraction particulate organic matter (CF POM) $> 53\,\mu m$ was determined using size fractionation by shaking soils with 10% w/v sodium hexametaphosphate for 4 h, then passing contents through a 53 μm sieve (Wander, 2004). Contents collected on sieves were transferred to metal weighing tins and dried for 24 h at 65°C. Organic C and N contents were determined using a VarioMax C/N analyzer (Elementar, Mt. Laurel, NJ) and reported as % C or % N.

Microbial Biomass C

Microbial biomass C (MBC) was determined by chloroform-fumigation extraction technique (Brookes et al., 1985; Vance et al., 1987). Total C of microbial biomass extracts was determined using a Shimadzu TOC-L/TN analyzer (Shimadzu, Kyoto Prefecture, Japan). Microbial biomass C was calculated by subtracting the total C in non-fumigated samples from total C in fumigated samples, corrected for initial soil moisture levels and amount of soil reacted. Microbial biomass C levels were not corrected for extraction efficiency, therefore representing a comparative flush of C across treatments rather than total microbial biomass (Fierer and Schimel, 2002).

Potentially Mineralizable N and Extractable N

Potentially mineralizable nitrogen (PMN) was determined using a 7-day anaerobic incubation technique, based on Drinkwater et al. (1997). Total extractable N was determined using Shimadzu TOC-L/TN analyzer pre- and post-incubation. PMN was calculated by subtracting the total N in baseline (pre-incubated) samples from total N in incubated samples. Values were corrected based on amount of dry soil reacted in solution. The initial baseline extractable N, which consists of mineral and dissolved organic forms of N, is hereafter referred to as EXTN.

Statistical Analyses

Soil parameters were analyzed using a mixed effects model with cover crop, time, and cover crop × time as fixed effects and block as a random effect (SAS 2006). Significant treatment by site by year interactions prevented pooling across locations and years, so each was analyzed separately. ANOVA model assumptions of normal variances and homoschedasticity were evaluated using residual plots.

Square root transformations were performed in PER Y1 for POMC, POMN, and PMN, in ANN Y1 for POM, and in ANN Y2 for EXTN and log-transformations were conducted for EXTN in PER Y1 to meet ANOVA assumptions. Means and standard errors were back-transformed (Jorgensen and Pedersen, 1998). Mean differences within each site by year combination in biomass, soil, and yield parameters were compared across cover crop treatments using *post-hoc* Tukey's HSD tests. All figures were made using the {ggplot2} package in R (Wickham, 2009).

RESULTS

Time of sampling and cover crop treatment were the two independent variables evaluated in this study. Time of sampling considerably impacted soil parameters, with $p < 0.05$ in 20 out of 24 soil parameter by site by year combinations (**Table 3**). In contrast, cover crop treatment did not impact soil parameters in most cases, and the NOCC control did not differ from some, or all, of the cover cropped treatments. For example, POMC, POMN, and MBC were not affected by cover crops, except in ANN Y1. Similarly, POXC was not affected by cover crop planting in any site-year. Cover crop by time interactions occurred most frequently for EXTN (PER Y1, $p < 0.001$; ANN Y1, $p < 0.001$; ANN Y2, $p = 0.007$) and did not occur for POXC or POMN parameters. Overall cover crop performance, quantity, and quality in this experiment are described in Perrone et al. (2020), showing considerable differences in biomass produced each study year. To briefly summarize, ANN Y2 exhibited the overall highest biomass production, with treatments yielding 4.6–9.3 Mg ha^{-1}, while PER Y2 exhibited the least amount of overall biomass, with treatments ranging from 0.2–4.9 Mg ha^{-1}. In PER Y2, substantial winter kill occurred. Vetch monocultures contributed among the greatest total N from aboveground biomass across all site by year combinations, and clover contributed among the lowest amounts of total N due to overall lower biomass production.

Time was a significant factor for POXC across environments except ANN Y1. From pre- to post-termination, POXC decreased in PER Y1 and ANN Y2, but increased in PER Y2, when cover crops performed poorly. Similarly, the time at which soil was sampled affected MBC in all sites and years, as well as POMC and POMN in all sites and years excluding PER Y2, again when biomass production was lowest. In all cases where sampling time was significant, POMC and POMN decreased after termination. Surprisingly, the inclusion of cover crop biomass quantity, defined as the amount of aboveground material produced by cover crop treatments, as a covariate did not affect any soil parameter and thus was omitted from analysis.

Cover crop species effects on soil responses after termination were mixed across sites, years, and response variables (**Table 3**). In particular, vetch production impacted extractable soil N (EXTN), with EXTN increasing more in VET plots than RYE and CLO plots in a majority of site by year combinations following cover crop biomass incorporation (**Figure 1**). Approximately 2

TABLE 3 | Mixed-model analysis of variance of permanganate oxidizable carbon (POXC), potentially mineralizable nitrogen (PMN)[a], extractable N (EXTN)[a,b], particulate organic matter C and N (POMC and POMN)[a], and microbial biomass C (MBC) due to cover crop species (CC), time, and CC x time.

Environment	Fixed effects	POXC	PMN	EXTN	POMC	POMN	MBC
		$F_{(dfn,dfd)}$					
PER Y1	CC	ns[c]	$5.97^{***}_{(4,69)}$	$19.85^{***}_{(4,64)}$	ns	ns	ns
	Time	$7.31^{***d}_{(2,102)}$	$306.49^{***}_{(1,69)}$	$250.99^{***}_{(1,64)}$	$4.63^{*}_{(2,100)}$	$5.32^{**}_{(2,99)}$	$37.53^{***}_{(1,66)}$
	CC x Time	ns	$6.11^{***}_{(4,69)}$	$16.57^{***}_{(4,64)}$	ns	ns	ns
ANN Y1	CC	ns	$4.77^{***b}_{(4,66)}$	$7.45^{***}_{(4,69)}$	$3.00^{*}_{(4,99)}$	$3.33^{*}_{(4,100)}$	$3.12^{*}_{(4,65)}$
	Time	ns	$46.63^{***}_{(1,66)}$	$56.04^{***}_{(1,69)}$	$7.41^{***}_{(2,99)}$	$6.54^{**}_{(2,100)}$	$89.27^{***}_{(1,65)}$
	CC x Time	ns	$3.40^{*}_{(4,66)}$	$9.03^{***}_{(4,69)}$	$3.80^{***}_{(8,99)}$	ns	ns
PER Y2	CC	ns	ns	ns	ns	ns	ns
	Time	$8.43^{***}_{(2,42)}$	$45.62^{***}_{(1,27)}$	ns	ns	ns	$7.81^{**}_{(1,30)}$
	CC x Time	ns	ns	ns	ns	ns	ns
ANN Y2	CC	ns	$4.16^{**}_{(4,34)}$	$7.60^{***}_{(4,34)}$	ns	ns	ns
	Time	$26.22^{***}_{(2,54)}$	$11.39^{**}_{(1,34)}$	$4.51^{*}_{(1,34)}$	$3.87^{*}_{(2,54)}$	$3.38^{*}_{(2,52)}$	$4.57^{*}_{(1,36)}$
	CC x Time	ns	ns	$4.17^{**}_{(4,34)}$	ns	ns	$2.69^{*}_{(4,36)}$

[a] *Square root transformations were performed in PER Y1 for PMN, POMC, and POMN, in ANN Y1 for POM, and in ANN Y2 for EXTN.*

[b] *Log-transformations were conducted for EXTN in PER Y1.*

[c] *ns = Not significant at $\alpha = 0.05$.*

[d] **, **, *** represent significance of F tests at $\alpha = 0.05$, 0.01, and 0.001, respectively.*

weeks post-termination, EXTN was 2 times greater in VET than in CLO and RYE treatments in ANN Y1. The following year (ANN Y2), the difference was 11.5 times greater (means presented in **Supplementary Material**). In PER Y1, EXTN in VET was 35% higher than CLO and RYE post-termination. Treatments RYE and CLO consistently exhibited among the lowest soil EXTN post-termination, in some cases lower than NOCC, suggesting N immobilization.

Potentially mineralizable nitrogen varied by site, year, time, and cover crop species (**Figure 2**), but few clear trends were evident. In PER Y1—the year that land was converted from unmanaged perennial grasses to annual crop production and cover crop biomass production was highest—PMN increased following cover crop termination and incorporation in all treatments relative to the NOCC control ($p < 0.001$). In PER Y2, when little biomass was produced, all plots showed a sharp decrease in PMN post-termination, as compared to levels pre-termination, by ∼50% ($p < 0.001$). For many soil parameters, PER Y1 exhibited greater overall values than in other site-years. For example, EXTN and PMN were considerably greater at PER Y1, with post-termination EXTN values ∼5 times greater, and post-termination PMN values ∼3 times greater, in Y1 than Y2. Additionally, POMC was ∼1.75 times higher in PER Y1 than all other site-years.

DISCUSSION

Cover Crop Impacts on C and N Pools Were Generally Modest

We hypothesized that despite relatively short establishment and maturation periods, cover cropped treatments would impact short-term soil nutrient cycling dynamics following spring termination, and would differ in their soil responses based on amount of biomass contributed to soils. Instead, winter cover crop treatments drove only minimal changes to soil C and N pools relative to the no cover crop control, with no observed differences correlated to the relative amounts of biomass contributed.

In Y1 at the perennial history site, EXTN in all plots increased following termination. This included increased EXTN in the no-cover crop control, but the degree of increase in the control was less than in cover cropped plots, suggesting some impact from mineralization of new biomass in cover cropped plots. In the same site and year, PMN increased in all plots except the no-cover crop control, suggesting the high biomass produced in this year increased the pool of plant available N that can be mineralized from labile SOM pools over the long-term. This site had a unique management legacy in that plots were established on an abandoned field, where perennial grasses had dominated for at least two decades until field preparations in summer 2014. Since perennial vegetation can increase organic N stocks (Cambardella and Elliott, 1992; Kantola et al., 2017), while landscape conversion rapidly reduces oxidizable C stocks and microbial biomass (DuPont et al., 2010), it is possible that soil disturbance resulting from plot management, cover crop termination, and mechanical weed control required in organic systems increased mineralization rates of existing protected and stabilized organic matter pools at this site in the first year of the study. However, since we did not include an undisturbed control in our experiment, the effect of disturbance-related management practices on C and N pools remains speculative. The higher percentages of POMC and POMN, a fraction largely comprised of leaf and root fragments (Wander, 2004), observed at the perennial history site pre-termination in Y1 in comparison to all other site-years may also be related to this landscape legacy.

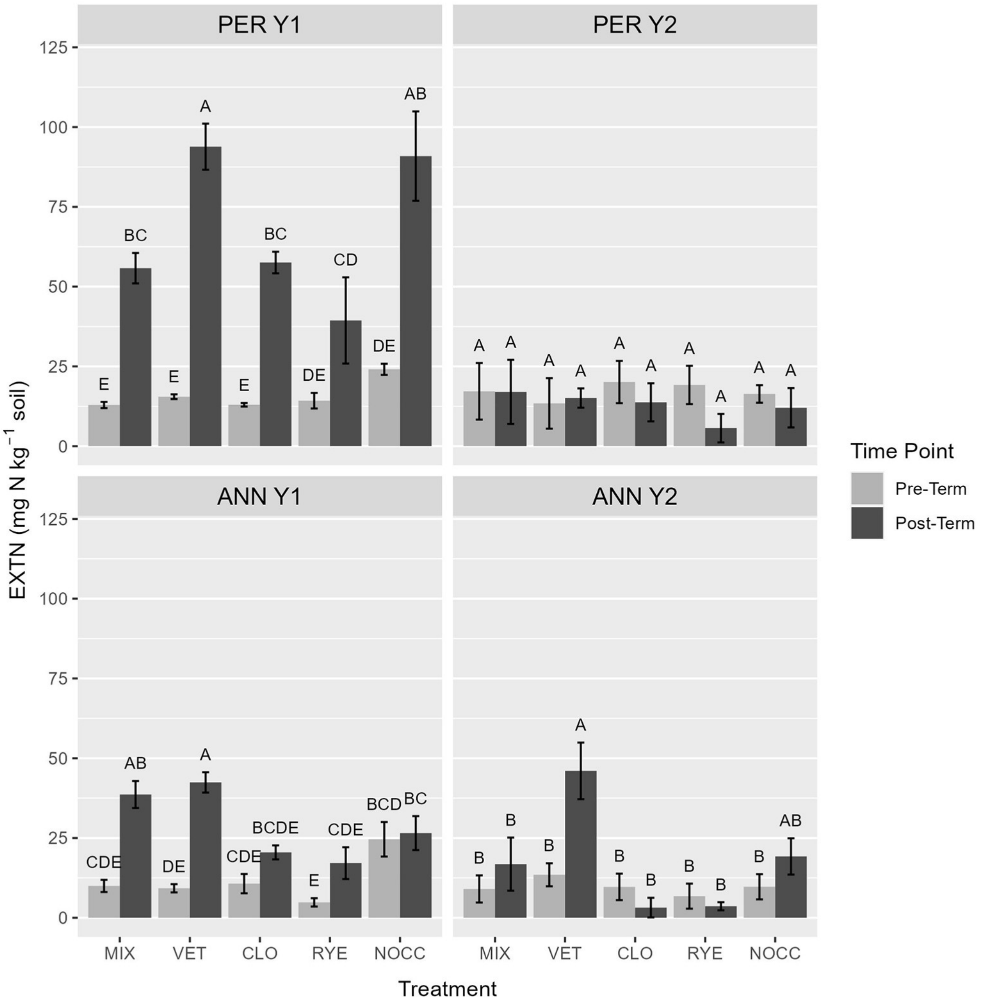

FIGURE 1 | Extractable nitrogen (mg N kg soil^{-1}) at experimental environments pre- vs. post-termination. Letters represent means separation within environment performed using a Tukey Honest Significant Difference *post-hoc* test (α = 0.05). Error bars indicate plus or minus one standard error of the mean.

This increased POM persisted to a lesser extent in Y2 at that location, with no effect of time of sampling on observed values. Notably, both POMC and POMN also declined after cover crop termination in both years at the annual cropping history site.

Permanganate oxidizable C is thought to be a source of labile carbon that is sensitive to changes in agricultural management (Culman et al., 2012), but less is known about individual species effects on POXC. While evidence suggests cover crop species can affect POXC and that an interaction between species and sampling time may exist (Ghimire et al., 2019), we found no effect of cover crop species on POXC in our study. Instead, POXC was influenced by location and sampling time. At the perennial history site in Y1, POXC was higher than other reported cultivated agricultural fields (Diederich et al., 2019), possibly due to the plot's management history and long-term legacy of living roots in the soil (Ginakes et al., 2020). Values of POXC in Y2 at this site are more typical for a soil under annual crop production (Diederich et al., 2019). At the perennial site in Y2, an early snowfall followed by an atypical freeze-thaw cycle in the fall (**Supplementary Material**) reduced winter survival of cover crops and may have accounted for the lack of influence of cover crop treatments on soil parameters. Indeed, VET and CLO treatments experienced significant winter kill, while RYE only produced about 63% of the biomass from the previous year, and roughly half the biomass as the annual cropping history site (Perrone et al., 2020). It is also possible that measurable impacts on the observed C pools may occur beyond the sampling timeline of this study as cover crop residue undergoes further decomposition, for example after the 2 week window between termination and sampling (Sievers and Cook, 2018).

The absence of cover crop biomass quantity and species impact on soil C parameters contradicts long-term evidence from corn cropping systems showing correlations between higher total C inputs and soil C (Coulter et al., 2009), yet likely reflects the need for decomposition models that reflect the interaction between microbial functioning and

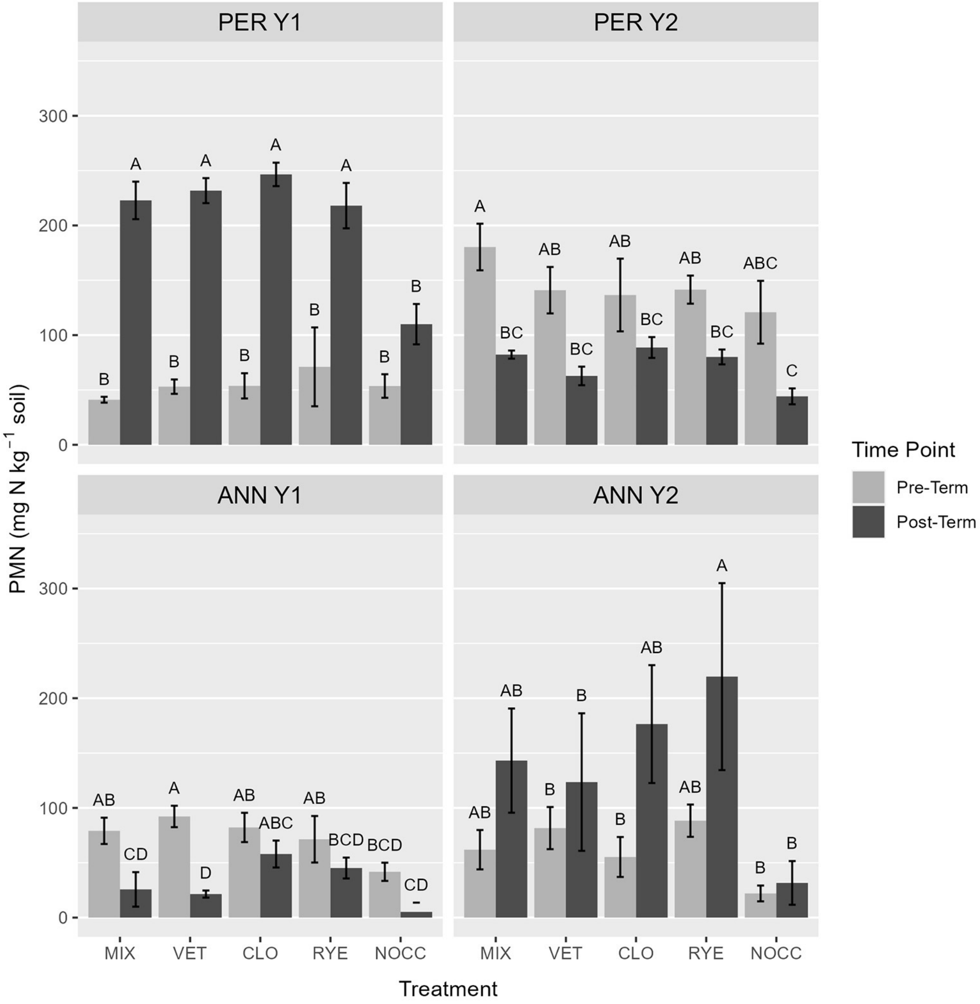

FIGURE 2 | Potentially mineralizable nitrogen (mg N kg soil^{-1}) at experimental environments pre- vs. post-termination. Letters represent means separation within environment performed using a Tukey Honest Significant Difference *post-hoc* test (α = 0.05). Error bars indicate plus or minus one standard error of the mean.

biomass quality, as well as macrobiotic and abiotic influences on SOM transformations (Wieder et al., 2014; Campbell and Paustian, 2015). That is, influences such as microbial community composition, biochemical characteristics of crop residues, invertebrate population dynamics, and soil temperature and moisture may be more likely to change over a 2-week period and therefore illustrative of short-term soil changes due to residue incorporation. These complex models are especially needed in systems that rely on ecological nutrient management and may be distinct in organic systems and those utilizing legume inputs.

Functioning of Legumes in Temperate Zone Horticultural Crop Agroecosystems

The vetch treatment had the strongest effect on soil N parameters in this study. Data supported that while most cover crop treatments impacted EXTN to some degree, especially in Y1 at both sites, the vetch treatment consistently ranked among the highest EXTN post-termination. Further, according to a recommendation of >25 ppm (Peterson, 2020), the amount of EXTN in vetch plots 2 weeks after termination was sufficient to fertilize a sweet corn crop at the perennial history site in Y1 (76.55 ± 7.15 mg N kg^{-1} soil), the annual cropping history site in Y1 (42.43 ± 2.14 mg N kg^{-1} soil), and the annual cropping history site in Y2 (39.16 ± 4.50 mg N kg^{-1} soil; see **Supplementary Material**). Vetch biomass at the perennial history site in Y2 was low, likely impacting the low EXTN observed after termination at this site and year. Overall, the amount of N released and measured as EXTN by cover cropped treatments in our experiment is similar to other studies employing winter annual legumes (Kuo and Sainju, 1998; St. Luce et al., 2013) and general crop residues (Christensen and Olesen, 1998). Potentially mineralizable nitrogen was comparable across both legume and grass treatments in almost all site-years, suggesting that legumes and grasses may not differ in terms of contribution of soil organic N in the form of PMN over short decomposition windows, especially when total biomass N values are similar.

Cover Crops and Ecological Nutrient Management in Vegetable Systems

This study showed only marginal contributions of winter cover crops to soil N and C pools in systems growing longer-duration vegetable crops, such as sweet corn, 2 weeks after termination. Although cereal rye and similar cool-season grasses remain the most common cover crops in cooler climates (Singer, 2008), opportunities for diversifying northern vegetable rotations with legumes and less common non-legume species exist, but face management challenges. In fall-planted cover crop systems, weed biomass is frequently greater in legume and brassica monocultures compared to grasses, driven by greater growing degree days that support weeds during early germination of weakly-competitive fall cover crops (Baraibar et al., 2018). When grown in mixtures, legumes are frequently outcompeted by non-legume components (Lawson et al., 2013; Wauters et al., 2021), reducing the value of legumes as an ecological nutrient management strategy. Clearly, work is needed to optimize legume success. Despite this competition, a metanalysis of cover crop N accumulation showed N content of hairy vetch-cereal rye mixtures to be 150% greater than that of cereal rye monocultures (Thapa et al., 2018), indicating a clear N benefit if optimization of legume performance can be realized. Laboratory incubations further support that that "fine-tuning" of nutrient delivery may be possible, where a pure hairy vetch and a 75% rye-25% hairy vetch mixture were found to release similar amounts of N after 70 days, with the initial release of N from the pure vetch stand higher than the mixture (Lawson et al., 2013).

Integration of cover crops with a diversity of available vegetable cash crops, each with unique days to maturity, could provide unique timing windows for cover crop inclusion in rotation between shorter duration crops. Horticultural systems thus may allow one to "mix and match" cash and cover crop species to fit available fallow periods. However, vegetable farmers in the Upper Midwest often grow multiple consecutive vegetable crops during the short growing season, which makes inclusion of cover crops into short rotational planting windows challenging if systems are intensified with fewer crops and higher acreages (Brainard et al., 2013; Moore et al., 2016). To best take advantage of the flexibility that vegetable rotations can offer, alternative rotational systems must be further explored. For example, cover crops inserted into short planting windows between cool season spring and fall vegetable crops could take advantage of a summer fallow period that, in cooler regions, is too short to cultivate a longer-duration warm season crop such as tomatoes or peppers. However, such cover cropping methods may reduce yields of subsequent crops, illustrating the challenges of cover crop integration in intensive horticultural systems in temperate zones. When comparing broccoli yields following short season (30–50 d) summer-planted cover crops in Minnesota and Wisconsin, yields in bare plots were found to be 30% higher than any cover cropped treatment in MN ($p = 0.062$), and 26% in WI ($p = 0.096$; Wauters et al., 2021). Clearly, optimization of warm season cover cropping systems in cool northern climates is still needed.

Ecological nutrient management in vegetable systems is undeniably complex, since the many opportunities for cover crop inclusion means that residue will be provided in varied amounts at different points in the growing season, thereby interacting with key drivers that govern nutrient provision via mineralization, including seasonal soil moisture and temperature. Our study provided data to support that even with short growing seasons that may limit aboveground biomass accumulation, winter cover cropping could provide benefits to soil N pools in the spring following termination, especially to slow N pools such as potentially mineralizable nitrogen. Because organic systems frequently suffer from N deficiencies, augmenting both available and organic forms of N via cover crops could improve crop yields via ecological nutrient provision (Berry et al., 2002; Drinkwater and Snapp, 2007), ultimately serving as a model to improve capacity for global food production.

CONCLUSION

Our study results suggest that cover crops, especially vetch, planted in colder northern climates during winter fallow periods can supply N following spring termination and contribute to longer term pools of labile C and N, but that these outcomes are highly dependent on site history and specific climatic events. The utilization of cover crops in locations with long winter seasons, regions which often intersect with the most productive and intensified agricultural regions in the U.S., provides an opportunity to shift agricultural paradigms toward greater farmer reliance on ecological nutrient management strategies. However, complex modeling of SOM transformations may be needed to optimize cover crop benefits. Data that supports introduction of cover crops into a wide range of vegetable production systems (organic, sustainable, or otherwise) will ultimately support a broad but often overlooked audience of farmers in adopting practices that supply nutrients to cash crops. A call to action to address SDG 2 is not only improved understanding of ecological nutrient management through research efforts, but also parallel farmer encouragement to understand and apply such principles in their farming context.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

SP and AL were graduate students on the project and lead all fieldwork, and co-contributed to manuscript body. AL wrote the original draft and SP significantly modified later versions. JG supervised graduate student field experiments, project design, and reviewed and edited multiple drafts of the manuscript.

NJ supervised graduate students and contributed to drafts of the manuscript. SW led statistical analysis. TS contributed to conceptual framework of process, experimental design, and development of figures. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.712152/full#supplementary-material

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How the Nitrogen Economy of a Perennial Cereal-Legume Intercrop Affects Productivity: Can Synchrony Be Achieved?

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The UN's Sustainable Development goal of Zero Hunger encompasses a holistic set of targets that range from ending hunger by 2030, to increasing environmental sustainability and resilience of food production. Securing and managing soil nutrients remains one of the most basic challenges to growing adequate food while simultaneously protecting biodiversity and the integrity of ecosystems. To achieve these objectives, it is increasingly clear that the management of ecological processes will need to supplant reliance on non-renewable and environmentally damaging inputs. In recent years, progress has been made in developing perennial grain crops that show promise to improve on a range of ecological functions such as efficient nitrogen cycling and soil carbon accretion that tend to be well-developed in natural ecosystems but become compromised following land conversion to row crop agriculture. Here we report on a multi-faceted, 5-year experiment in which intermediate wheatgrass (IWG) (*Thinopyrum intermedium*), a perennial relative of wheat that is bred to produce the grain Kernza®, was intercropped in alternating rows with the perennial legume alfalfa (*Medicago sativa*). The performance of the unfertilized intercrop was compared to monocropped IWG treatments, with and without urea-N applications, planted at two row densities such that the intercrop could be interpreted as either an addition or substitution design. Comparisons of relative IWG yields (RYs) in the intercrop with unfertilized monocrops suggest net competitive interactions between alfalfa and IWG in the establishment year, followed by increasing degrees of facilitation over the next 4 years. Evidence from N fertilizer responsiveness, SPAD readings, net N mineralization assays, and N balance calculations suggest that alfalfa contributed to an aggrading pool of soil organic nitrogen over the course of the experiment. Comparisons of grain RYs of intercropped IWG and fertilized IWG monocultures suggest N-limitation in the first half of the experiment, and N sufficiency in the second half. Grain yields in the intercrop did not decline significantly over 5 years in contrast to all IWG monocrop treatments that did significantly decline. This study contributes to a growing literature on approaches to ecological nutrient management that incorporate diversity and perenniality to increase food security and resilience.

Keywords: alfalfa, intermediate wheatgrass, Kernza®, perennial grain, UN Sustainable Development Goal, zero hunger, ecological nutrient management

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INTRODUCTION

Input intensification characterized many of the most consequential agricultural innovations of the 20th century. For example, the invention and widespread adoption of synthetic nitrogen fertilizers was a pre-requisite for the quadrupling of the human population between 1920 and 2020 (Smil, 2001; Davidson et al., 2012). While profound in the outsized role they have played in feeding humanity, adoption of N fertilizers also resulted in outsized environmental problems as the amount of reactive N cycling in the ecosphere has exceeded what many believe to be a safe planetary boundary (Rockstrom et al., 2009; Steffen et al., 2015). A principal reason for these environmental problems is that only about half of applied N fertilizers are taken up by crops (Ladha et al., 2005; Lassaletta et al., 2016). The other half either leach into aquatic ecosystems, often inducing eutrophication, or are emitted in gaseous forms that have local to global consequences, including the formation of potent greenhouse gasses and the destruction of stratospheric ozone (Galloway et al., 2004; Howarth et al., 2005). In addition to environmental challenges, the economic consequences of fertilizer dependence for famers and ultimately consumers can be unpredictable. For example, due to the volatility of natural gas markets underlying N fertilizer production supplying sub-Saharan Africa, the average cost of urea has increased more than 300% between November 2020 and November 2021, resulting in lower fertilizer application rates and lower food production by farmers [IFDC (International Fertilizer Development Center), 2022].

Considering the social and environmental costs that have been associated with strategies of input intensification in general, and adoption of N fertilizers in particular, researchers are increasingly envisioning agroecosystems that maintain productivity through manipulation of ecological processes (Foley, 2011; Bommarco et al., 2013; Kleijn et al., 2018; Cassman and Grassini, 2020). Indeed, achieving sufficient food production through approaches like ecological nutrient management while reducing inputs that harm the environment are in close accord with the United Nation's Sustainable Development Goal of Zero Hunger by 2030 (United Nations, 2021; Target 2.4). Intercropping cereals with legumes is a time-tested approach to ecological nutrient management that is receiving renewed interest globally (Malézieux et al., 2009; Li et al., 2011; Lithourgidis et al., 2011; Pelzer et al., 2017; Daryanto et al., 2020). Much of this interest lies in the potential to improve on the synchrony between N supply and demand in cereal cropping systems (Gardner and Drinkwater, 2009), as well as shifting reliance from fossil fuel-intensive industrial sources of fixed nitrogen to biological nitrogen fixation (Crews and Peoples, 2004, 2005).

Several mechanisms have been identified to explain how diversifying cereal production with the inclusion of a compatible legume can improve on N synchrony in annual crops. While belowground transfer of N from annual legumes to cereals due to rhizodeposition of exudates (Fustec et al., 2010), root or nodule turnover (Johansen and Jensen, 1996), direct root contact (Hupe et al., 2021) or interspecific mycorrhizal bridging (Ayres et al., 2007; Meng et al., 2015) have been detected within a growing season, most evidence suggests that such transfers are minor relative to mechanisms of N partitioning (Bedoussac et al., 2015; Rodriguez et al., 2020). Annual cereals have been found to be more competitive than annual legumes in taking up available soil N, inducing greater reliance by legumes on N fixation (Rodriguez et al., 2020). Cereals are therefore thought to access more N on a per plant basis in many intercrop settings because of this shift from soil to atmospheric N sources by legumes coupled with a lower density (plants per hectare) of cereal plants in replacement intercrop designs (Rodriguez et al., 2020).

Perennial Crops and Ecological Nutrient Management

In annual intercrops, mechanisms by which legumes might contribute to improved N synchrony in cereals, are restricted to those that might occur within a growing season. Perennial cereal-legume intercrops that maintain deep roots over years represent a category of emerging cropping systems that potentially expand on the ecological nutrient management mechanisms that underlie annual cereal-legume intercrops. In this study we investigated the nitrogen economy of an intercrop consisting of perennial intermediate wheatgrass [IWG; *Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey] that is undergoing *de novo* domestication to produce the grain Kernza®, with the perennial legume alfalfa (*Medicago sativa,* L.). We hypothesize three mechanisms that may facilitate a perennial cereal-legume intercrop such as IWG and alfalfa to achieve greater synchrony of soil N supply and crop demand.

1) *Enhanced soil N uptake efficiency*. Established stands of IWG have consistently reduced nitrate leaching relative to annual grains by 77–99% (Culman et al., 2013; Jungers et al., 2019; Reilly, 2021). The ability to take up greater soil N in time and space equates to more complete utilization of existing soil N resources, potentially leading to improved synchrony (Blesh and Drinkwater, 2013; Ruan et al., 2016).

2) *Enhanced legume N fixation*. Annual legumes, whether intercropped for grain, green manure or forage, have been found to fix less nitrogen, or fix less consistently across years compared to perennial forage legumes that begin the growing season fully established and commonly fix N for longer durations per year (Peoples et al., 2012; Schipanski and Drinkwater, 2012).

3) *Enhanced soil organic N accumulation*. The amount of N fixed by an annual legume that can be transferred to an associated cereal crop is limited by processes governing N enrichment of the soil organic nitrogen pool (Ayres et al., 2007; Crews et al., 2016). Perennial legumes have the potential to build SON pools through years of continued N fixation and rhizodeposition of N-rich exudates, roots and nodules (Fustec et al., 2010).

When considered together, these mechanisms suggest that perennial cereal-legume intercrops may benefit from greater N inputs from biological N fixation (BNF), reduced N losses and a resulting accumulation of larger pools of organic-N with the potential for mineralization to better synchronize with crop N demands (Drinkwater and Snapp, 2007).

The intercrop advantage in annual cereal-legume systems is weighted toward a net reduction in competition as the interaction between the two functional groups enhances legume utilization of atmospheric N and cereal utilization of soil N (Jensen et al., 2020). Under these circumstances, the yield (biomass or grain) of either individual species in the intercrop would be expected to be lower than monocropped fields planted at an equivalent density to the intercrop since the resource partitioning of N in the intercrop is enhanced but not complete; some competition for soil N remains. A net reduction in competition through resource partitioning of N has also been found to occur in perennial grass-legume intercrops (Schipanski and Drinkwater, 2012), and given that inputs from legume N fixation can accrue over years, perennial intercrops also have the potential to experience net facilitation whereby the legume both reduces reliance on and contributes to soil N reserves available to the cereal. In this case the non-legume species in the intercrop may show greater productivity than it achieves in a monocrop, as the legume contributes the limiting resource of N (Vandermeer, 1990; Bybee-Finley and Ryan, 2018).

The goal of the current study was to understand competition and facilitation as well as resource partitioning in a perennial legume-cereal intercrop with a special emphasis on N dynamics. Specifically we asked:

1. Is there evidence of resource competition or facilitation when intermediate wheatgrass is intercropped with the perennial legume alfalfa? Do these interactions change over time? Do these interactions change when the intercrop is a replacement vs. an addition design?
2. To what extent does the N uptake potential of intermediate wheatgrass synchronize with the N supplied by the intercropped legume alfalfa? What evidence is there that alfalfa is supplying N to IWG? Do alfalfa shoots and roots both contribute to enhancing soil organic N pools and in turn IWG productivity?
3. How does the mass balance of the annual and cumulative N budget of the intercrop system compare with fertilized and unfertilized single species stands of intermediate wheatgrass?
4. Does efficient N cycling translate into reduced emissions of the greenhouse gas nitrous oxide?

MATERIALS AND METHODS

Study Site and Experiment Establishment

Research plots were established in October of 2012 at The Land Institute in central Kansas, USA (38°49'20.13" N; 97°35'29.51" W). In the USDA taxonomy, soils were coarse-silty, mixed, mesic Fluventic Haplustolls in the Cozad silt loam series (Palmer et al., 1992). The site receives an average of 760 mm of precipitation per year with 70% falling as rain between April through September. The average high and low temperatures for July are 34 and 20.5°C, and in January are 4 and −7°C. The site is considered semi-arid with soil moisture deficits occurring in most years and topsoil pH values ranging from 7 to 8.

Four replicates of seven treatments were sowed into recently tilled land that was previously planted to an unfertilized perennial sorghum. Plots measuring 5.2 m (L) × 6 m (W) were sowed to single species stands of IWG consisting of 13 rows per plot, or intercrops of IWG and alfalfa consisting of seven rows of IWG alternating with 6 rows of alfalfa. A buffer row of IWG spaced at 38 cm was sowed between treatments. Intermediate wheatgrass seed was "Cycle 2," an early breeding population from The Land Institute. Treatments were sown as follows:

1. IWG = single species, no fertilizer, sowed in 76 cm rows
2. IWG+N = single species, 75 kg urea-N ha^{-1} yr^{-1}, sowed in 76 cm rows
3. IWG(2) = single species, no fertilizer, sowed in 38 cm rows
4. IWG(2)+NP = single species, 150 kg urea-N and 20 kg triple super phosphate-P ha^{-1} yr^{-1}, sowed in 38 cm rows
5. IWG-ALF = alternating rows of IWG and alfalfa sowed in 38 cm rows, no fertilizer
6. IWG-ALFr = alternating rows of IWG and alfalfa sowed in 38 cm rows, no fertilizer, alfalfa shoot biomass removed with root biomass remaining.
7. IWG-ALFs = single species (IWG only), no fertilizer, sowed in 76 cm rows, mulched with ALF shoot biomass produced in the plots of treatment 6.
8. IWG-ALFu = alternating rows of IWG and alfalfa sowed in 38 cm rows, 20 kg P ha^{-1} yr^{-1} as human urine, sowed in 38 cm rows.

The seeding rate for IWG plots was 6 and 12 kg ha^{-1} for IWG(2) plots. In the bicultures, alfalfa was seeded at a rate of 4.5 kg ha^{-1}. Alfalfa seed variety was "I-70" and was inoculated with rhizobia. By establishing two row spacings of single species intermediate wheatgrass plots, both fertilized and unfertilized, it was possible to interpret the design as a *replacement* strategy, where one row of IWG in the 38 cm row spacing was replaced with a row of alfalfa, and as an *addition* strategy, where alfalfa was added to the intermediate wheatgrass planted in 76 cm rows (**Figure 1**) (Bybee-Finley and Ryan, 2018). Triple super phosphate was included in treatment 4 as a fertilizer-based comparison to treatment 8, which consisted of urine as a P source. Treatment 8 was discontinued in 2014 due to logistical challenges. Over a decade of breeding intermediate wheatgrass had taken place at this research site and in no cases had breeding populations shown responsiveness to P fertilizer amendments although responses to N additions have been common (DeHaan, pers com). In the interpretation of results in this study, we are confident in focusing on N dynamics, although we cannot rule out P effects in the IWG(2)+NP treatment.

Experiment Management and Productivity Measurements

Fertilizers were applied to the soil surface of plots between March 15 and April 25 of every year. Alfalfa produced 2–4 cuttings per year (2, 4, 3, 2, 2 cuttings from 2013 to 2017, respectively) as influenced by stand age, climate and interactions with IWG. Every year in early May initial alfalfa growth was lost to herbivory by newly emerged alfalfa weevils (*Hypera postica*). Thereafter, at ca. 10% flowering, alfalfa biomass was cut by hand and replaced as mulch either back on original plots (IWG-ALF) or removed from IWG-ALFr plots and placed between rows of IWG in IWG-ALFs plots. During harvest, the alfalfa biomass from two 5.2 m rows were weighed and subsampled for dry:wet

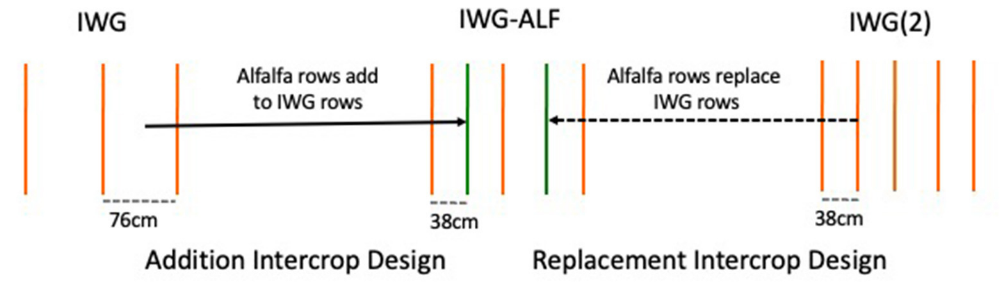

FIGURE 1 | Addition and replacement designs for comparing IWG-ALF intercrops with IWG monocrop treatments.

conversions (see below). Each year in the third week of July, 1-m sections of aboveground biomass + seed of IWG were cut from two rows by hand to 4 cm stubble height to estimate aboveground net primary production (ANPP) in all treatments. Within days, grain was harvested with a Wintersteiger (Delta) plot combine, dried, cleaned, and weighed. In every alfalfa and IWG plot harvest, subsamples of biomass were taken directly from the field, weighed, dried at 60C until constant weight, and weighed again to obtain dry:wet weight conversion ratios for estimating ANPP on a dry weight basis. IWG and alfalfa subplot harvests were scaled to hectare equivalents for comparisons. After grain harvest IWG residues were swathed, baled, and removed. Determination of δ^{15}N and %N were made on alfalfa and IWG shoot materials sampled in early June ~6 weeks before harvest. Shoots from five plants per plot of each species present were sampled and aggregated into one composite sample. At harvest, IWG stems and seeds were sampled from all treatments for %N determination. All shoot materials harvested for N analyses were dried at 60°C and knife milled to homogenize bulk plant materials. Subsamples were ball milled, weighed into tin capsules and sent to SIMSL stable isotope laboratories at Kansas State University for determination of %N and δ^{15}N.

We calculated relative yields (RY) (Vandermeer, 1990), also referred to as partial Land Equivalent Ratios (Bybee-Finley and Ryan, 2018) to compare the relative ANPP and grain harvests of IWG in the addition and replacement intercrop designs.

$$\text{IWG RY} = \text{IWG harvest}_{\text{intercrop}}/\text{IWG harvest}_{\text{monocrop}}$$

IWG RY values <1 indicate that the yields of IWG in the intercrop are lower than those of a IWG monocrop grown on an equivalent land area, implying competition. RY values >1 indicate that IWG yields in the intercrop exceed those of a monocrop grown on an equivalent land area, implying facilitation (Vandermeer, 1990; Bybee-Finley and Ryan, 2018).

Net N Mineralization

In 2015, we measured potential N mineralization of soils from IWG-ALF, IWG(2), and IWG(2)+NP in field and laboratory incubations after Robertson et al. (1999). To conduct field incubations, we cut schedule 80, 5 cm dia. PVC pipe into 23 cm lengths, and beveled one end. Two sets of two tubes were hammered, beveled end down, 20 cm into the soil between 12" crop rows. Two of the four tubes were immediately extracted and put on ice. The remaining two cores were capped with PVC caps and left in the field. In the laboratory, the extracted soils were transferred from the PVC tubes to plastic bags where they were homogenized. Within 24 h of sampling, a 5 g subsample was removed from each bag and placed in 50 mL of 1 M KCl, shaken for 2 min, shaken again for 1 min after 4 h, and then sampled by pipette after 20 h for NH_4^+ and NO_3^- analyses. A separate ~10 g sample was removed from each plastic bag, weighed, dried at 100°C for dry weight conversion. The remaining field cores were retrieved after 25–35 days and processed the same as the initial cores.

To undertake N mineralization incubations of soil strata deeper than 20 cm, we used a hydraulic soil corer to obtain 5 cm(D) × 1 m(L) cores, which we divided into the following strata: 1–10, 10–20, 20–40, 40–60, 60–80, and 80–100 cm. Soil samples were placed in plastic bags, homogenized by hand and subsampled for KCl extractions as described above. A separate 5 g sample from each sample bag was placed in a petri dish, and based on oven-weight conversion values, each stratum's moisture content was adjusted to 40% moisture using reversed osmosis water in a spray bottle. Soils were kept in the dark and adjusted to 40% moisture on a daily basis throughout the incubation period. After 25 days, the samples were extracted with 1M KCl. KCl samples were frozen until analyzed, along with field N mineralization KCl extracts, by the Kansas State soil testing laboratory for nitrate and ammonium concentrations. Average daily potential net N mineralization was calculated as:

$$N_{\text{mineralized}} = \frac{[(\text{Nitrate}_f - \text{N} + \text{Ammonium}_f - \text{N}) - (\text{Nitrate}_0 - \text{N} + \text{Ammonium}_0 - \text{N})]}{t_{\text{days}}}$$

where Nitrate_f and Ammonium_f = final nitrate and ammonium N concentrations. Nitrate_0 and Ammonium_0 = initial nitrate and ammonium N concentrations.

Estimation of N Fixation by Alfalfa

We designed the experiment to employ the natural abundance of ^{15}N method for estimating N-fixation over the course of the study (Unkovich et al., 2008). Central to the method is the

TABLE 1 | Relative Yield[a] (RY) ratios of IWG ANPP grain yields grown in addition replacement intercrop designs with alfalfa (IWG-ALF) relative to four monocrop IWG treatments.

Intercrop design	IWG treatment	Harvest category	Year				
			2013	2014	2015	2016	2017
Addition	IWG	ANPP	0.9	1.1	1.2	1.4	1.9
Addition	IWG+N	ANPP	1.1	0.9	0.9	0.8	0.9
Addition	IWG	Grain	0.8	0.9	1.1	1.2	3.4
Addition	IWG+N	Grain	0.8	0.6	0.7	1.0	1.2
Replacement	IWG(2)	ANPP	0.8	1.1	1.5	1.9	2.7
Replacement	IWG(2)+NP	ANPP	0.7	0.5	0.7	0.8	1.0
Replacement	IWG(2)	Grain	0.7	1.0	2.3	1.8	4.2
Replacement	IWG(2)+NP	Grain	0.7	0.6	1.1	1.1	1.4

RY ratios <1 suggest net competition ratios >1 suggest net facilitation influences IWG productivity in the intercrop relative to monocrop treatments.

[a] *Relative Yield of IWG = Intercrop IWG harvest$_{intercrop}$/IWG harvest$_{monocrop}$.*

calculation of percent nitrogen derived from the atmosphere (%Ndfa) as follows:

$$\%\text{Ndfa} = \frac{\delta^{15}\text{N IWG} - \ \delta^{15}\text{N alfalfa}}{\delta^{15}\text{N IWG} - \ \beta} \text{ x } 100$$

where IWG was used as the non-N_2 fixing reference plant selected to approximate the spatial and temporal patterns of soil N uptake by alfalfa. There is a general consensus that the natural abundance of ^{15}N method is only viable when the reference and legume $\delta^{15}N$ differ by a minimum of 2 delta units (Unkovich et al., 2008). Year one (2013) was the only year this criterion was met, and thus was the only year we fully calculated %Ndfa (88%) and total shoot N fixation based on field derived ^{15}N values. For years 2–5, we used a hybrid approach to estimate N fixation that integrated field values for shoot %N and total biomass, with a %Ndfa value of 70% (median value, n=120 alfalfa fields in Europe; Anglade et al., 2015). As a check on our approach to estimating shoot N fixation, we used correlations between alfalfa shoot dry weight and N fixation reported by Carlsson and Huss-Danell (2003) in Europe and North America (**Table 1**). To estimate above + belowground inputs of N derived from alfalfa N fixation we used an alfalfa-specific conversion factor based on aboveground N fixation of 1.61 (Walley et al., 1996).

Root Collections

In 2013 and 2014, one meter soil cores measuring 6.2 cm in diameter were removed from IWG(2), IWG(2)+NP and IWG-ALF plots to quantify root biomass with depth. Cores were partitioned with a knife into two 10 cm strata (0–10 and 10–20), and then four 20 cm strata. Four hundred grams of soil at field moisture were twice passed through a 6 mm sieve to collect coarse roots. Next the 400 g soil samples were passed through a 1 mm sieve using a gentle spray of water, leaving fine roots on the mesh for collection. Coarse and fine roots were dried at 60°C and weighed.

Nitrous Oxide Measurements

We used static chambers in IWG(2), IWG(2)N+P and IWG-ALF treatments to collect gas samples for nitrous oxide analyses approximately every 2 weeks from May 12-Sep 15 in year 3, and April 18-Oct 3 in year 4, with additional sampling events added following fertilization and rain events. Molded PVC chambers 25 cm in diameter were placed on PVC rings inserted 2 cm in the soil, and air was sampled from the chamber four times over a 45-min period. Chamber air samples were collected in nylon syringes and stored up to 24 h before analysis. In the laboratory N_2O was analyzed using a gas chromatograph (Agilent 6890) fitted with an electron capture detector (ECD) and calibrated with certified N_2O standards. N_2O flux was calculated as the increase in concentration within the chamber over 45 min.

SPAD Index Measurements

We used a Minolta SPAD-502 to measure chlorophyll content of intermediate wheatgrass in mid-June of years 2 and 3 of the experiment. Measurements were taken on 15 leaves per replicate and averaged resulting in four replicate values per treatment. The SPAD meter was positioned mid-length on the second fully expanded new leaf of sampled plants.

Statistical Analysis

We used separate repeated-measures mixed linear model analyses (PROC MIXED, SAS 9.4) to test for differences over time among total IWG ANPP and grain yields among primary treatments (IWG-ALF, IWG, IWG(2), IWG+N, IWG(2)+NP). The ANPP and grain yield were square root-transformed to provide best fit for the mixed models. Next, we used repeated-measures mixed linear models to analyze IWG yield effects over time for different avenues of alfalfa N-transfer (IWG-ALF, IWG-ALFs, IWG-ALFr, IWG). For these models ANPP was ln-transformed and grain yield was square root-transformed to provide best model fit. In both models, treatment was the fixed variable and year was the random repeated variable (subject = treatment*replicate, with an AR(1) covariance matrix).

To determine total N_2O emissions from treatments IWG(2), IWG(2)+NP, and IWG+ALF in 2015 and 2016, we calculated the area under the curve (AUC) for N_2O flux by treatment plot by year using the equation:

$$AUC = \sum_{t_0}^{t_{final}} [(x_t + x_{t+1})/2]*[(t+1) - t]$$

where t_0 is initial sampling date, t_{final} is final sampling date, x_t is the N_2O flux at given time t, and x_{t+1} is the N_2O flux at the next sampling date.

Once AUCs were calculated for each plot by year, we analyzed effects of treatment, year, and treatment*year interaction on total N_2O emissions using a two-way ANOVA with treatment as a fixed effect and year and treatment*year included as random effects. The AUCs were ln-transformed in order to meet the assumptions of normality and variance homogeneity. We then conducted follow-up pairwise comparisons with a Tukey-Kramer adjustment to determine differences by treatment.

Treatment effects on SPAD, net N mineralization and root biomass measurements taken in individual years were analyzed with one-way ANOVAs using JMP 11 (SAS, Cary, North Carolina, USA). When the effect of the treatments was found to be significant (*F*-tests, $p < 0.05$), means were compared using Tukey's HSD test at $\alpha = 0.05$.

RESULTS

ANPP and Grain Yield

ANPP of IWG changed significantly over time for all treatments, being greatest in the initial year and lowest in the final year of the experiment (**Figure 2A**, **Supplementary Table S1**). These yield extremes corresponded to the highest and lowest precipitation extremes, respectively, for April-July measured over the 5 years (**Supplementary Figure S1**). The decline in productivity between 2013 and 2017 was greatest in unfertilized IWG treatments, such that by 2017, these treatments had significantly lower ANPP than fertilized IWG treatments (**Figure 2A**). Decreases between 2013 and 2017 for IWG ANPP were 87% [IWG(2)], 78% (IWG), 68% (IWG(2)+NP), and 47% (IWG+N). When alfalfa was included, the ANPP of the IWG-ALF intercrop reached peak biomass in year 2, and then declined by 37% between years 2014 and 2017. In contrast to aboveground biomass production, grain yields in treatments that experienced N additions peaked in Year 2 (2014), whereas IWG and IWG(2) peaked in year 1 (2013) (**Figure 2B**). Mean grain yields decreased significantly over 5 years in all IWG monocrop treatments while we measured no significant decrease in yields of the intercrop over the 5-year study (**Figure 2B**).

Replacement and Addition Intercrop Designs

The design of this experiment allowed us to evaluate the performance of the IWG-ALF intercrop both as a replacement and addition to IWG monocrop configurations (**Figure 1**). In both designs, intercrop grain and biomass productivity were intermediate between the fertilized and unfertilized IWG treatments (**Figures 2A,B**). When interpreted as a replacement design (IWG-ALF compared to IWG(2) or IWG(2)+NP treatments) differences between the intercrop and monocrop were strongly dependent on whether supplemental fertilizers were applied to the monocrops. From 2014 to 2017, IWG(2) demand for N and possibly P appeared to exceed the nutrients supplied through soil resources alone, as IWG(2)+NP ANPP was significantly greater than IWG(2) ANPP from 2014 to 2017. In the establishment year, N did not appear to strongly limit IWG(2) productivity. Intermediate wheatgrass ANPP in the IWG-ALF intercrops was relatively low in the establishment year, but by 2014, ANPP equaled that of IWG(2) even though the intercrop had half the intermediate wheatgrass planting density. By years 3–5, the effect of the alfalfa became more pronounced as intercrop productivity increasingly exceeded that of unfertilized IWG(2). The differences in intermediate wheatgrass ANPP between IWG(2)+NP and IWG-ALF were large in the first 2 years (between 3–4 tons ha^{-1} yr^{-1}) but then narrowed over the final 3 years to where ANPP of these two treatments was equal in 2017. When the ANPP of IWG and alfalfa were summed (IWG+ALF total) the unfertilized intercrop shared the ranking of most productive treatment with the fertilized IWG(2)+NP for four of the 5 years (**Figure 2A**).

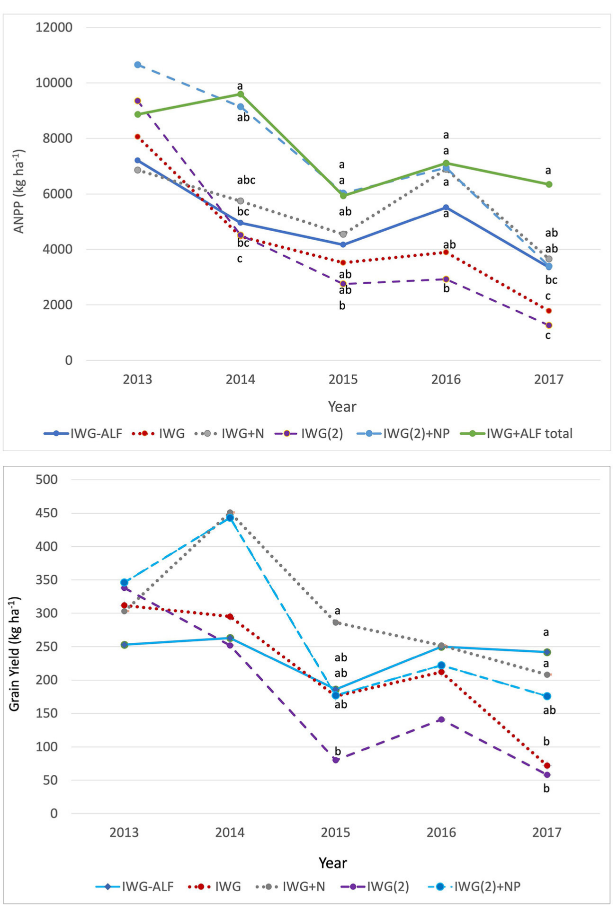

FIGURE 2 | Productivity of IWG as influenced by crop density, diversity, and fertility treatments. **(A)** Aboveground net primary productivity (ANPP) of IWG (kg ha^{-1}) in monoculture and biculture treatments as well as ANPP of IWG-ALF including alfalfa (IWG+ALF total–green line) for all years, and **(B)** Grain yields of IWG (kg ha^{-1}) in monoculture and biculture treatments for all years. Different lowercase letters represent significant differences within years ($P < 0.05$) based on Tukey pairwise comparisons.

When interpreted as an addition intercrop experiment, the row of alfalfa in the IWG-ALF treatments represents an addition to the IWG monocrop treatments (IWG and IWG+N) planted at 76 cm row spacing. This addition of alfalfa resulted in an intercrop with double the crop density of the monocrop IWG treatments. Patterns of mean intermediate wheatgrass ANPP in the intercrop addition comparisons were similar but less exaggerated than the patterns exhibited in the replacement design. In 2013, the IWG-ALF treatment had lower ANPP and grain yield than either fertilized or unfertilized IWG and the reduced grain yield persisted through year 2 (**Figure 2B**). These differences in productivity occurred when N appeared to be relatively abundant, thus competition for water may have occurred. By 2015, the IWG-ALF ANPP was greater than the unfertilized IWG plots, and grain production of these two treatments was similar. The IWG+N treatment produced the highest ANPP and grain production of the wide-spaced IWG (**Figure 2A**).

Compared to patterns of ANPP, grain yields differed considerably when evaluated as replacement and addition intercrop designs. In the replacement comparison, grain yields of the intercrop were about 30% lower than fertilized or unfertilized IWG(2) plantings in year 1 (2013) (**Figure 2B**). In 2014, IWG(2)+NP grain yields peaked, but then declined precipitously in 2015, and remained low but stable from 2016 to 2017, whereas yields of unfertilized IWG(2) declined substantially after the establishment year. Grain yields in the intercrop were quite consistent at ca. 250 kg ha^{-1} yr^{-1} for four of the 5 years. In the addition comparison, both fertilized and unfertilized IWG treatments had greater mean grain yields than the intercrop in 2013 and 2014, but the trend reversed in the later years of the experiment with mean intercrop grain yields exceeding IWG monocrops in 2017 (**Figure 2B**).

Relative Yield Comparisons

Relative yield (RY) ratios help to clearly distinguish intercrop performance relative to fertilized and unfertilized monocrops (**Table 1**). In 2013, seven of the eight different IWG intercrop vs. monocrop comparisons showed that the monocrops yielded greater biomass or grain, resulting in RYs <1 (i.e., it would require less land under a monocrop to achieve the IWG yield of the intercrop). With the sole exception of the 2016 IWG(2) grain RY, the annual increase of IWG RYs was evident for ANPP and grain comparisons of unfertilized treatments in both addition and replacement intercrop designs (**Table 1**). RYs in the final year of the experiment were particularly high at 3.4 and 4.2 in the unfertilized addition and replacement intercrops, respectively. In contrast to comparisons with unfertilized IWG treatments, RYs involving fertilized IWG treatments changed less after 2013. ANPP RY ratios in the addition intercrop stayed almost constant between 0.8 and 0.9, with grain ratios increasing from 0.6 to 1.2. In the fertilized replacement intercrop after the establishment year, ANPP RYs dropped to 0.5 and then increased to 1.0 from 2014 to 2017, and the grain ratios dropped to 0.6 in 2014 and then gradually increased to 1.4 in 2017.

Alfalfa N Fixation

Estimations of N inputs into the IWG-ALF treatment from alfalfa N-fixation ranged between 54 and 162 kg ha^{-1} yr^{-1} (**Table 2**). The shoot N fixation value of 55 kg N ha^{-1} for 2013 that was based entirely on field measurements was similar to the value of 52 kg N ha^{-1} calculated using a correlation of shoot fixed N and alfalfa dry matter production reported by Carlsson and Huss-Danell (2003). N fixation estimates for 2014–2016 were lower than the correlation-based estimates whereas the two approaches produced the same value of 80 kg N fixed ha^{-1} in 2017. The reduced fit between field-based N fixation estimates and the correlation check can be explained by lower alfalfa shoot %N in years 2014–2016 compared to 2013 and 2017 (**Table 2**).

TABLE 2 | Shoot %N, total-N and fixed-N in alfalfa from the IWG-ALF treatment between 2013–2017 based on empirical and literature values.

Year	Aboveground Alfalfa Biomass				Shoot + Root
	%N	Total-N	Fixed-N	Correlation check[a]	Fixed N[b]
		KgN ha^{-1}			
2013	3.77	62	55[c]	52	89
2014	3.10	144	101[d]	114	162
2015	3.06	54	38[d]	54	61
2016	3.02	48	34[d]	50	54
2017	3.81	114	80[d]	80	129

[a] *Estimations of kg N fixed ha^{-1} check based on correlations of shoot N fixed per ton of dry biomass from Europe and N. America: N fixed = $16.9+21^{*}$tons alfalfa DM, $R^2 = 0.91$ (Carlsson and Huss-Danell, 2003).*

[b] *Belowground fixed N in alfalfa was estimated using a root factor of 1.61 (Fixed N in roots is ~80% of shoots) (Walley et al., 1996).*

[c] *Year 1 N fixation was calculated using alfalfa $\delta^{15}N$ values and IWG from IWG-ALF as the reference; %Ndfa = 88%.*

[d] *A %Ndfa of 70% was used in place of an empirically derived proportion based on the median value of alfalfa from 120 farm sites in Europe (Anglade et al., 2015).*

Addition of Alfalfa Root and Shoot to IWG

The addition of alfalfa roots, shoots or roots+shoots to unfertilized, wide spaced IWG rows did not result in statistically different levels of ANPP, and seed yields were only significantly different between the root + shoot and no-alfalfa treatments in the final year (**Figure 3**, **Supplementary Table S2**). Both ANPP and grain yield of the no-alfalfa treatment had the highest mean values in the first year and declined over time to the lowest mean values in the final year.

N Balance

The N balances for each year of the experiment were calculated as managed N inputs in urea or alfalfa N fixation minus N exported in harvest. Predictably, the two treatments that received neither of the N inputs, IWG and IWG(2), maintained negative N balances for all 5 years of the experiment (**Figure 4A**). The degree of N deficit mirrored the patterns of biomass and grain exports with the most negative N balances in 2013, and the least negative in year 2017. The IWG+N and IWG(2)+NP had small negative N balances in year one of −26 and −15 kg ha^{-1}, respectively, but in subsequent years IWG(2)+NP maintained a greater N surplus than IWG+N ranging between 42 and 91 kg ha^{-1}. The mean N balance of the IWG-ALF intercrop varied substantially from year to year reflecting the relative productivity and N fixation by alfalfa relative to IWG productivity through time. The intercrop experienced N deficits of 20 kg ha^{-1} in 2013 and 17 kg ha^{-1} in 2016, with N surpluses of 119, 34, and 90 kg ha^{-1} in years 2014, 2015 and 2017, respectively.

The mean cumulative N balances of managed inputs minus harvested exports over 5 years revealed an almost identical negative slope for the IWG and IWG(2) non-fertilized treatments even though row spacing and seeding rates differed by 100% (**Figure 4B**). IWG at both row spacings exhibited maximum productivity and thus the greatest N deficit in 2013, followed by N balances between −65 and −11 kg

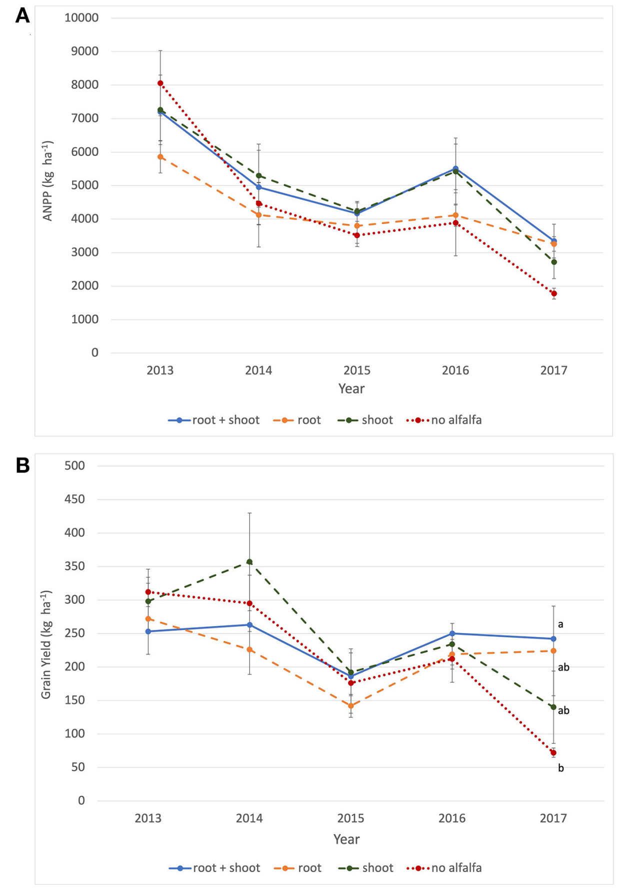

FIGURE 3 | Influence of above and belowground alfalfa biomass on IWG productivity. **(A)** Mean ANPP and **(B)** mean grain yield of IWG planted in 76 cm rows with the following inter-row alfalfa additions: root+ shoot, root only, shoot only, none. No within year differences of ANPP between treatments were found to be statistically significant. In grain yields, different lower-case letters represent significant differences within years ($P < 0.05$) based on Tukey pairwise comparisons. Bars = 1 S.E.

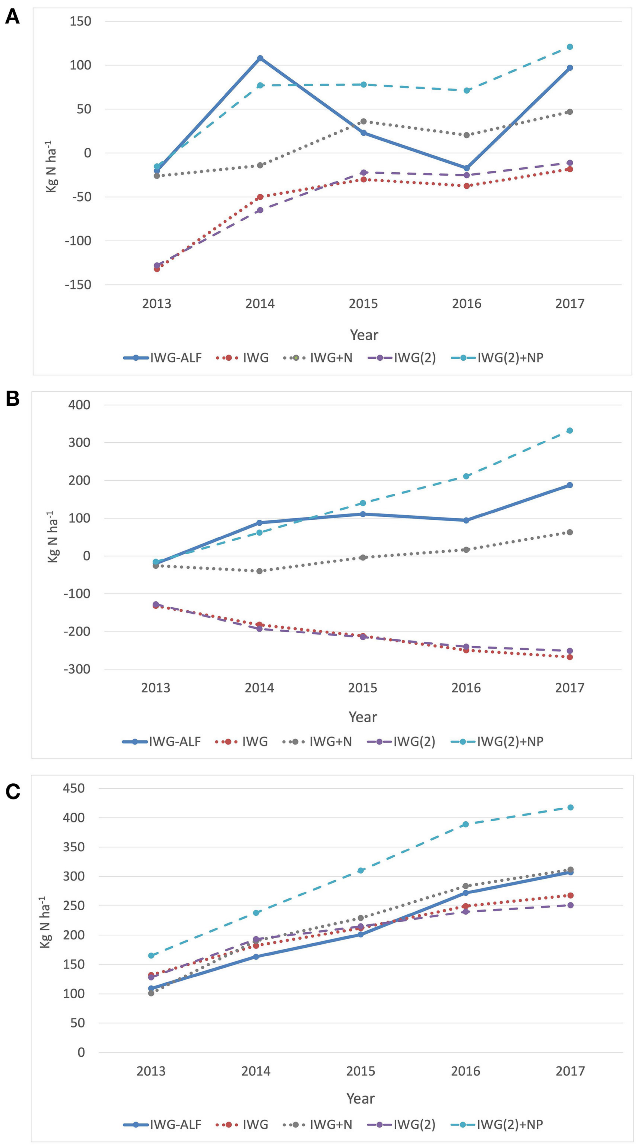

FIGURE 4 | N balance comparisons of intercropped IWG-ALF with unfertilized and fertilized IWG treatments. **(A)** Yearly N balance calculated as managed N inputs in urea or alfalfa N fixation minus N exported in harvest, **(B)** Cumulative N balance over 5 years, **(C)** Cumulative N export in grain + biomass harvests over 5 years.

ha^{-1}, corresponding to increasingly N-limited yields over the following 4 years. The three treatments that received N inputs—IWG+N, IWG(2)+NP and IWG-ALF–demonstrated positive cumulative N balances over 5 years of 63, 332, and 188 kg ha^{-1}, respectively.

Differences between cumulative N exported between 2013 and 2017 from the unfertilized IWG and IWG(2) treatments compared to the IWG-ALF treatment were 39 and 56 kg ha^{-1}, respectively (**Figure 4C**). In contrast, five-year cumulative net N balance differences between IWG-ALF and the IWG and IWG(2) unfertilized treatments were 456 and 439, respectively (**Figure 4B**).

Total N Export

The mean N exports in biomass and grain harvests from all treatments except IWG(2)+NP were similar (within 35 kg) for the first 3 years of the experiment (**Figure 4C**). In the final 2 years the IWG+N and IWG-ALF treatments appeared to bifurcate from the two non-fertilized IWG treatments, showing greater N exports, presumably in response to receiving N inputs. The IWG(2)+NP treatment mean N offtake was the highest of all treatments in all years, with an export of 165 kg N ha^{-1} in 2013, followed by 3 years of between 70 and 80 kg N ha^{-1} yr-^{1}, and then a sharp decline to 29 kg N ha^{-1} in 2017.

SPAD Index

By measuring the difference between the transmittance of a red (650 mn) and infrared (940 nm) light through leaves,

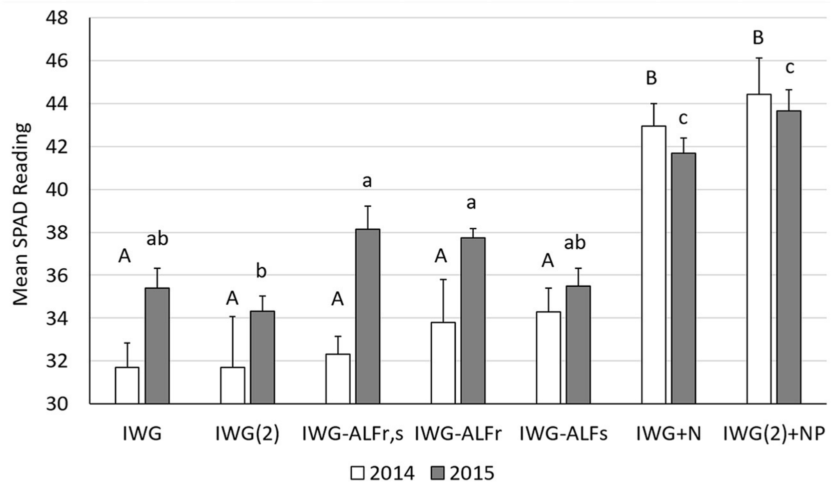

FIGURE 5 | SPAD values reflecting relative IWG leaf N status as influenced by crop density, diversity, and fertilization in 2014 and 2015. Bars with different upper and lower-case letters indicate significant differences between treatments in 2014 and 2015, respectively, at $p < 0.05$ (Tukey HSD). SPAD values from both years were log transformed to achieve normal distributions (not shown).

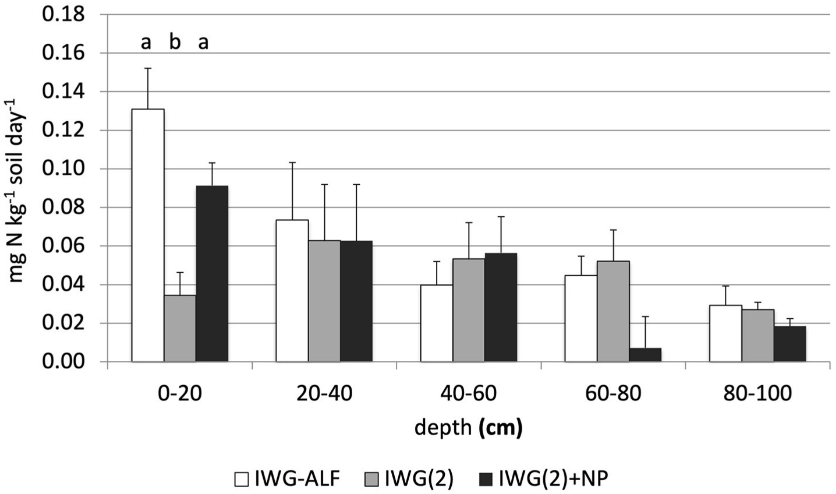

FIGURE 6 | Net N mineralization assay conducted in year three of IWG-ALF, IWG(2) and IWG(2)+NP treatments. Laboratory incubation of 1 m cores obtained in early July, which were divided into five-20 cm strata. Bars with different lower-case letters indicate significant differences at $p < 0.05$ (Tukey HSD). Bars = 1 S.E.

SPAD meters calculate relative values of chlorophylla+b content which can be directly related to the N status of a crop (Yuan et al., 2016). In 2014 of the experiment, significantly different mean SPAD values of IWG were measured between the urea-N addition treatments and all others [ANOVA $F_{(6,26)} = 13.83$, $P < 0.0001$] (**Figure 5**). By 2015, the mean SPAD values of IWG had differentiated to a greater extent showing significantly greater chlorophyll content of IWG-ALFr,s and IWG-ALFr treatments compared to unfertilized IWG(2) and significantly less than both fertilized IWG treatments [ANOVA $F_{(6,26)} = 22.66$, $P < 0.0001$] (**Figure 5**).

Net N Mineralization

In 2015, laboratory incubations of soils sampled to 1 m depth from IWG+ALF, IWG(2) and IWG(2)+NP treatments were undertaken to compare rates of net N mineralization. The intercrop treatment IWG+ALF and the fertilized treatment IWG(2)+NP were found to support significantly greater rates of net N mineralization than the unfertilized IWG(2) treatment in the surface 20cm of soil (**Figure 6**, **Supplementary Table S3**). Below 20 cm, no significant differences were found between treatments. In the same treatments in 2015, we conducted *in situ* soil net N mineralization assays to 23 cm depth across 4 months from spring to late

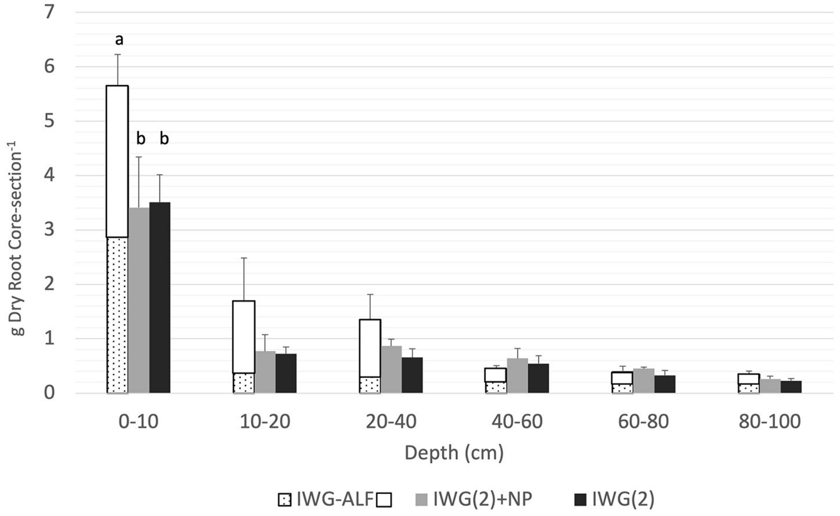

FIGURE 7 | Mean total root biomass (coarse + fine roots) sieved from two 1 m cores (diameter 6.2 cm) per plot in 2015. In the IWG(2)+NP treatment (gray bar) and the IWG(2) treatment (black bar) 1 core was sampled from 2 separate rows. In the IWG-ALF treatment, 1 core was sampled from an alfalfa row (white) and one core sampled from an intermediate wheatgrass row (speckled). In all cases cores were taken from between plants. Cores were divided into six strata. Bars with different lowercase letters indicate significant differences within a depth at $p < 0.05$ (Tukey HSD). Bars = 1 S.E.

summer (**Supplementary Figure S2**, **Supplementary Table S4**). Mean net N mineralization rates were higher in the IWG-ALF treatments compared to unfertilized IWG in each of the 4 month-long assays, but none of the differences were statistically significant. Mean N mineralization in IWG-ALF and IWG(2)+NP treatments were equivalent in the first measurement of the summer, but were significantly lower than the fertilized treatment in Period 2 and exhibited a similar trend in the subsequent two periods. This finding reflects the timing of fertilization, as the first set of cores were installed on April 23, a week before urea applications to the IWG(2)+NP treatment.

Total Root Biomass in Intercrop vs. Monocrop Treatments

The IWG-ALF intercrops produced significantly greater mean total root biomass (fine + coarse) in the top 10 cm compared to IWG(2) and IWG(2)+NP plots in 2014 (not shown) [ANOVA $F_{(17,68)} = 10.19$, $P < 0.0001$] and 2015 (ANOVA $F_{(17,71)} = 26.43$, $P < 0.0001$] (**Figure 7**). In the 0–10 cm stratum of the intercrop treatments, the soil cores sampled from the IWG and alfalfa rows had similar total root biomass. However, in all depths below 10 cm, there was greater root biomass in the strata sampled from the alfalfa row. It was not possible to separate roots by species. We attempted to determine the proportion of alfalfa and IWG roots collected from the rows of the two species by analyzing their δ^{15}N signatures relative to pure samples of alfalfa and IWG roots. However, the difference in δ^{15}N values between alfalfa and IWG roots were insufficient, and intraspecific variation too great to characterize the composition of mixed roots from the cores (data not shown).

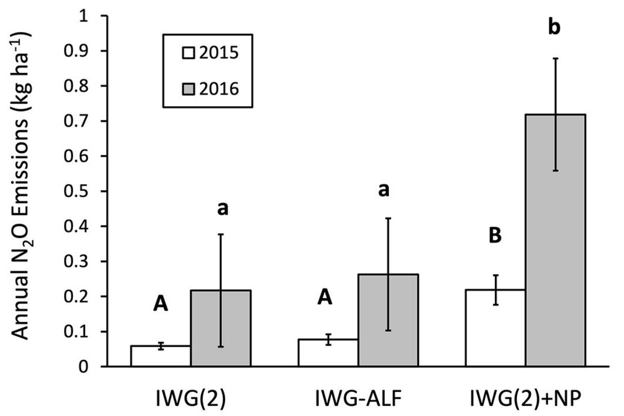

FIGURE 8 | N_2O emissions summed over growing season in 2015 and 2016 from IWG(2), IWG-ALF, and IWG(2)+NP treatments. Treatments with different letters indicate significant differences at $p < 0.05$ (Tukey HSD). Bars = 1 S.E.

Nitrous Oxide Emissions

Nitrous oxide emissions were significantly greater in the IWG(2)+NP treatment that received urea-N compared to the IWG(2) and IWG-ALF treatments in both 2015 and 2016 (**Figure 8**). The highest N_2O emissions were measured early in the growing season which corresponded to urea applications in the IWG(2)+NP treatment, as well as warmer soil temperatures and intermittent wet conditions (**Supplementary Figure S3**).

Change in δ^{15}N in IWG and Alfalfa

Significant differences in shoot δ^{15}N values were observed in Years 2013–2015 between alfalfa and IWG within the IWG-ALF intercrop, with IWG having higher δ^{15}N signatures than alfalfa.

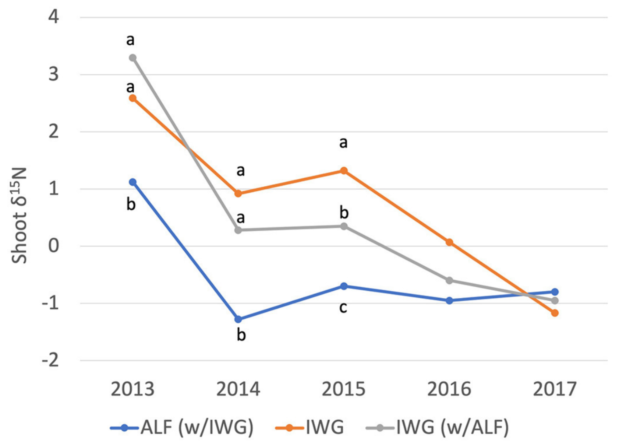

FIGURE 9 | Changes in shoot $\delta^{15}N$ over 5 years from IWG-ALF and IWG treatments in the replacement intercrop design. Crop designations are ALF (w/IWG) = shoots from alfalfa grown with intermediate wheatgrass, IWG = shoots from intermediate wheatgrass grown in monocrop, IWG (w/ALF) = shoots from intermediate wheatgrass grown with alfalfa. Bars with different lowercase letters indicate significant differences at $p < 0.05$ (Tukey HSD).

The two crop species did not differ in δ^{15}N in Years 2016 and 2017 (**Figure 9**, **Supplementary Table S5**).

DISCUSSION

Results from this 5-year study highlight important ways in which diversity and perenniality combine to influence the supply and cycling of N–two key targets of ecological nutrient management. Comparisons of IWG yields in addition and replacement intercrop designs with unfertilized IWG monocrops provided insight into a temporal shift from net competition in early years to net facilitation in later years governing IWG and alfalfa interactions. Similar comparisons of IWG intercrop yields with fertilized IWG monocrops revealed the degree to which alfalfa N fixation inputs were able to meet the N demands of associated IWG over time. These intercrop and monocrop comparisons, coupled with N balance and relative yield calculations, and indicators of N availability and crop N synchrony, provide a multi-dimensional understanding of ecological nutrient management in perennial cereal-legume intercrops.

Productivity

The greater productivity measured with fertilization of low and high density IWG plantings compared to unfertilized plantings demonstrated N limitation across all 5 years of the experiment. The rapid and precipitous decrease in ANPP and grain yield in the unfertilized and densely planted IWG(2) treatment suggests the development of profound N limitation (**Figure 2**).

Against the backdrop of fertilized and unfertilized IWG treatments, RYs of ANPP and grain production by IWG in the intercrop reveal important patterns relevant to ecological nutrient management. Intercropping IWG with alfalfa, in both addition and replacement configurations, resulted in RYs in the establishment year that were consistently <1 (**Table 1**), possibly due to belowground competition for water or nutrients when alfalfa and IWG have yet to partition niches via differential rooting depths. From 2015–2017, the RYs of all intercrop comparisons with unfertilized monocrops show clear evidence of net facilitation (**Table 1**). In absolute terms, the addition of alfalfa appears to slow the decline of ANPP demonstrated by IWG and IWG(2), and it prevents the decline of grain yields measured in the monocrop treatments (**Figures 2**, **3**). Yields in IWG monoculture stands have been found to decline in the first 2–3 years in other studies (Jungers et al., 2017; Hunter et al., 2020).

In response to the overarching question of whether intercropping with alfalfa results in sufficient N fixation and mineralization to meet the demands of IWG, the answer, based on yield comparisons with fertilized IWG treatments, is generally "no" early in the experiment, and generally "yes" late, but there are interesting differences between addition and replacement designs with respect to ANPP. Intercropped IWG in the addition experiment had ANPP yields similar to those of the fertilized monocrop over the 5 years of the study, suggesting weak to no N limitation in the intercrop. In contrast, the same ANPP comparison between intercropped IWG and the fertilized monocrop in the replacement design suggested N limitation to intercropped IWG in years one through four. Relatively low grain yields in the first 3 years of the intercrop implied moderate N-limitation in both the addition and replacement designs relative to fertilized monocropped IWG treatments. In contrast intercropped IWG grain yields in the second half of the experiment were equal or greater than fertilized monocropped IWG in both designs suggesting N sufficiency and a small degree of facilitation in the intercrop. It makes sense that the yields of intercropped-IWG in the replacement design might be less than fertilized monocultures, since the IWG plant density in the intercrop was half that of the monocrop. The finding that RYs in this comparison were >0.5 in the first 2 years, and >1 in the final three underscores how diversity can play a pivotal role in ecological nutrient management. It is not simply the provisioning of N by alfalfa that supports intercrop grain productivity, but also an apparent reduction in IWG intraspecific competition, or another ecological function such as pathogen suppression.

Other studies examining IWG-legume intercrop dynamics have also reported relatively lower IWG yields in intercrops compared to monocrops, especially when the intercropped legume was alfalfa or another species deemed to be competitive. Reilly (2021) found intercrops involving alfalfa and red clover (*Trifolium pretense*) tended to have relative yields <1 compared to unfertilized IWG. The row spacing used in Reilly's experiments was 15 cm, with 2 rows of legume for every 1 row of IWG (45 cm between IWG rows); much closer than the spacing used in the present study which may have enhanced competition and depressed RY values. Less competitive legumes such as Canada milkvetch (*Astragalus canadensis*) and white clover (*Trifolium repens*) did demonstrate positive RY values in the majority of sites and years (Reilly, 2021). When compared to fertilized IWG Reilly found IWG intercropped with six different perennial legumes grown in three sites for 3 years to have RYs < 1.

In a separate Minnesota study, Tautges et al. (2018) compared yields of unfertilized and N-fertilized IWG monocrops with a replacement design intercrop where every other row of IWG was replaced with alfalfa. In year 2 of the study, grain yields of the intercrop were lower in 3 of 5 locations compared to unfertilized monocrops, and 4 of 5 locations compared to fertilized treatments. The lower intercrop yields appeared to be the result of lower IWG density and in some cases, suppression of intermediate wheatgrass by alfalfa. Patterns of productivity changed by year 4 and yields of the intercrop were greater than unfertilized monocrop treatments in 4 of 5 locations and fertilized monocrop treatments in 3 of 5 locations (Tautges et al., 2018). Similar to the present study, the authors suggested the intercrop performance may have been tied to improved N fertility provided by the legume as alfalfa biomass was correlated positively with grain yield, harvest index and nutrient uptake in the year 4 intercrop.

Casamitjana (2021) recently reported on a project in which IWG productivity was evaluated as a function of row spacing, N fertility and legume intercrop in Wisconsin USA. She found that when legumes, including alfalfa, were added to IWG stands in addition intercrop designs, grain and ANPP either did not change or decreased. However, Casamitjana was only able to study wheatgrass-legume intercropped plots for 3 years which is before facilitation effects of alfalfa were detected in the present study and by Tautges et al. (2018). In SE Australia, Hayes et al. (2016) found replacement intercrop designs of perennial wheats and subterranean clover (*Trifolium subterraneum*) to yield less than addition designs. Replacing cereal rows with legumes resulted in greater N fixation inputs but the reduction in cereal stand density lowered intercrop yields compared to monocultures. The Australian experiment only lasted for 3 years and the authors acknowledged that the relative performance of the intercrop could change in later years.

The results from the experiment in which we partitioned the influence of above and belowground alfalfa inputs were not significant (**Figure 3**). In other studies, evidence increases that belowground inputs from root death and turnover have a greater influence than aboveground inputs on soil organic matter accretion (Rasse et al., 2005; Schmidt et al., 2011; Poirier et al., 2018), but we did not see that in this study. The relative roles of above and belowground inputs are relevant because a range of strategies are being considered to manage IWG-alfalfa intercrops. One involves removal of aboveground alfalfa biomass by hand or machine for animal forage, while another involves cutting the alfalfa and leaving it in place as an organic mulch for weed control and N addition. More research would be useful to determine whether legume shoot biomass removal affects IWG grain and biomass productivity and soil carbon accumulation.

N Synchrony

N synchrony has been defined as the matching of crop N demand with N supply (Robertson, 1997; Drinkwater and Snapp, 2007). The two common types of asynchronies that occur are when N supply falls short of or exceeds crop N demand (Crews and Peoples, 2005). Annual N balance and cumulative N balance calculations of the IWG monocrop and intercrop plots suggest that N demand in unfertilized plots strongly exceeded N supply. In contrast, N supply likely strongly exceeded crop demand in the IWG(2)+NP treatment where in years 2014–2016, about half of the 150 kg N ha-1yr^{-1} applied was not exported in crop biomass, increasing to 80% in 2017 (**Figure 4A**). While the annual N balance of the intercrop treatment fluctuated substantially between positive and negative across years, the cumulative mean N balance of the IWG+N, IWG-ALF and IWG(2)+NP treatments were positive by 63, 188, and 332 kg ha^{-1}, respectively. However, we know that estimated N fixation by a living perennial legume does not equate to "N supply" in the same time frame as applications of readily available N in the form of urea fertilizer. Biological processes such as root turnover and mineralization regulate the rate of legume-N release for cereal uptake, thus restricting the potential for N losses that negatively impact the environment. In contrast, fertilizer-N forms lack mechanisms of biological regulation, and thus surpluses are vulnerable to loss pathways that commonly result in ecosystem disservices such as eutrophication or enhanced N_2O emissions (Crews et al., 2016).

Our N balance calculations do not include N sinks associated with microbial immobilization in the short term, and net soil organic matter accumulation in the longer term that is predicted to take place with the conversion of annual cropping systems to perennial vegetation (Post and Kwon, 2000; Sprunger et al., 2017; King and Blesh, 2018). The duration of this experiment fell short of the time commonly considered necessary to detect significant differences in soil organic carbon stocks following a change in crop vegetation (Necpálová et al., 2014; McGowan et al., 2019). However, reviews and meta-analyses that examined soil carbon sequestration rates following the conversion of annual to perennial grasslands report a range of 0.3–1 ton C ha^{-1} yr^{-1} (Crews and Rumsey, 2017). Most stable soil organic matter (SOM) has C:N ratios of between 10 and 15:1, and thus the N required to accumulate 0.3–1 ton C ha^{-1} would fall between 20 and 100 kg N ha^{-1} yr^{-1} or 100–500 kg ha^{-1} over 5 years. If we assume this range of organic matter accumulation rates is applicable to perennial grain crops, then this potential N sink could account for the 5-year positive N balances of the IWG+N, IWG-ALF, and IWG(2)+NP treatments. Positive N balances on croplands that are in approximate equilibrium with SOM accumulation and loss rates may have greater potential to lose N, resulting in negative environmental impacts. However, agroecosystems undergoing successional changes such as the shift from annual to perennial grains will likely need to maintain positive N balances for up to decades until SOM pools achieve new equilibria (Crews et al., 2016).

N Dynamics of IWG-ALF Intercrop and Unfertilized IWG

The relative stability of ANPP and grain yields of the IWG-ALF intercrop compared to fertilized and unfertilized IWG monocrops across 5 years is noteworthy (**Figure 2**), especially when soil N dynamics appeared to change throughout the same period of time. It seems clear that when a perennial cereal and legume are sowed simultaneously, the plant and soil processes involved in N fixation and transfer from the legume to cereal require more than one growing season to develop (Louarn et al., 2015). Plant establishment, cycles of shoot cutting and residue decomposition, root and nodule turnover, and stand thinning all likely contribute to a gradually aggrading pool of soil organic nitrogen (Gault et al., 1995; Peoples et al., 2009; Louarn et al., 2015). In our study, several lines of evidence suggest that a consequential pool of organic N had accumulated by year 3 (2015) in the IWG-ALF treatment, and continued to facilitate IWG productivity through 2017. First, changes in SPAD meter readings from 2014 to 2015 (**Figure 5**) suggest an increase in IWG-ALF leaf chlorophyll content and N content by proxy relative to the unfertilized IWG treatments. Second, the net N mineralization lab assay conducted in 2015 suggests greater N supply from microbial mineralization in the intercrop soils compared to soils from IWG(2) (**Figure 6**). Third, cumulative N exports from the intercrop treatment fell below those of the unfertilized IWG treatments between 2013 and 2015, consistent with N limitation (**Figure 4C**), while during the same time, the cumulative N balance of the IWG-ALF intercrop was very similar to IWG(2)+NP, the treatment that received the greatest fertilizer inputs (**Figure 4B**). Only after 2015 did the cumulative N exports from the intercrop exceed those of the unfertilized treatments. That N inputs to the intercrop were high, but N availability was low for the first half of the experiment is consistent with the idea that N inputs were decoupled from N supply to IWG, resulting in an accumulation of soil organic nitrogen in the intercrop.

Other studies have reported on a similar decoupling of N inputs from perennial legumes and N supply to proximate perennial grasses. In a ryegrass (*Lolium perenne*) white clover (*Trifolium repens*) intercrop in Denmark, Hogh-Jensen and Schjoerring (1997) used ^{15}N enrichment and natural abundance methods to estimate that only 3% of the N fixed by clover was accessible to ryegrass in the first year of production. In the second and third years, as the soil organic nitrogen pool grew larger and N mineralization increased proportionately, this percentage increased to 17 and 22%, respectively. In another study involving N transfer from red clover (*Trifolium pratense*) to Kentucky bluegrass (*Poa pratensis*), Thilakarathna et al. (2016a) found that N fixation in red clover was greatest in the first production season, but seasonal N-transfer doubled in the second production year over the first. They attributed the increase in N transfer from legume to grass with stand age to increases in root mass and surface area, root exudates, senescence and decay of roots and nodules, defoliation induced N release by legume root systems, and development of mycorrhizal hyphae networks (Thilakarathna et al., 2016a,b). Decoupling of N inputs from perennial legumes has also been documented in alley cropping systems involving tree and/or shrub hedgerows bordering narrow fields of annual grains. Okonkwo et al. (2008) found single applications of prunings from *Gliricidia sepium* and *Leucaena leucocephala* to maize significantly increased net soil N mineralization by 2–3-fold over controls for three growing seasons in Nigeria. In a detailed review of the N budgets of similar alley cropping systems in tropical regions, Sanginga et al. (1995) estimated that N inputs in hedgerow prunings commonly exceeded 300 kg N ha^{-1} yr^{-1}, while only ∼30% or less appeared to be taken up by the cereal in the first year of the growing season. The authors surmised that the remaining N added to an aggrading pool of soil organic nitrogen, as we found in the IWG-ALF intercrop, or was lost to the environment, given windows of compromised N synchrony inherent in the annual cropping cycles. Although they acknowledged belowground N transfers are poorly understood and characterized, Sanginga et al. (1995) estimated that 25–102 kg N ha^{-1} season^{-1} were contributed by roots and nodule turnover of hedgerow legume species to the annual cereal.

Natural abundance of ^{15}N values from alfalfa and IWG in the intercrop and the unfertilized IWG treatment over 5 years suggests a shift from soil organic matter as the primary source of available N early in the experiment to more depleted inputs later in the experiment (**Figure 9**). In 2013, the mean δ^{15}N value of IWG shoots grown in the intercrop was relatively enriched at 3.3, and then declined over the next years converging on a δ^{15}N signature similar to that of the N-fixing alfalfa in 2017. This simple ^{15}N pool dilution interpretation of converging legume and grass δ^{15}N values cannot be used to demonstrate with certainty that soil pools of legume-fixed N are responsible for the change in intermediate wheatgrass δ^{15}N (Peoples et al., 2015). Indeed, this example is complicated because the δ^{15}N signature of the unfertilized monocropped IWG also declined over the course of the study even though it is not influenced by the less enriched δ^{15}N of alfalfa-N. We speculate that the relatively enriched δ^{15}N signatures of IWG from both monocrop and intercrop treatments in the establishment year (2013) reflected relatively high rates of soil N mineralization stimulated by the tillage employed to establish the experiment. The similar ANPP in 2013 of unfertilized IWG and IWG(2) treatments relative to their fertilized counterparts also supports the interpretation that endogenous N was sufficient early (**Figure 2**). In subsequent years, it is clear that the IWG(2) treatment became increasingly N limited exacerbated by annual removal of N in harvests, and reduced soil N mineralization with the cessation of soil disturbance. The δ^{15}N values of vegetation experiencing profound N limitation frequently reflect the δ^{15}N values of inputs as opposed to enriched soil δ^{15}N driven by N losses (e.g., Vitousek et al., 1989). In the case of central Kansas, δ^{15}N of nitrate and ammonium deposition has been measured at 2 to −15 (Townsend et al., 2003), thus N deposition is frequently strongly depleted in ^{15}N as compared to atmospheric N_2. We suggest that the decline in δ^{15}N in the IWG treatment may reflect a shift in relative dependence from mineralized soil-N to atmospheric deposition-N. It is likely that the intercrop IWG δ^{15}N also reflects atmospheric deposition, however the greater ANPP and grain yields produced by the intercrop compared to the unfertilized IWG treatments in years 4–5 imply that the δ^{15}N signature of legume N inputs likely contributed to the depleted δ^{15}N of intercrop IWG as well (**Figure 2**).

Root Biomass

The finding of significantly greater root biomass in the 0–10 cm stratum of the IWG-alfalfa intercrop compared to fertilized or unfertilized monocropped IWG(2) contributes to a growing body of literature showing a positive relationship between diversity and belowground productivity in experiments involving wild and domesticated perennial species (**Figure 7**). Yang et al. (2019) measured approximately twice the root mass in plots with two vs. one perennial species in 5 years after establishment. The combination of functional groups they found to produce the greatest root biomass were C_4 grasses and legumes. In a comparison of perennial monocultures of bioenergy crops such as miscanthus and switchgrass and diverse grassland systems, Sprunger et al. (2017) consistently found greater fine root production in the diverse grassland ecosystems. In the present study, greater total root biomass produced in the intercrop replacement design compared to IWG(2) monoculture treatments suggests that the alfalfa and IWG are avoiding competition through resource partitioning and/or there is facilitation of belowground productivity between species. More studies will be required to determine whether perennial cereal-legume intercrops consistently maintain higher root biomass compared to monocrop perennial cereals. The question is highly relevant to predicting rates and amounts of soil carbon accumulation and resulting nutrient retention in a transition from annual to perennial species (Sprunger et al., 2020).

Nitrous Oxide Emissions

In many respects it is not surprising that the IWG(2)+NP treatment sustained high N_2O emissions over two growing seasons in 2015 and 2016 compared to the unfertilized IWG(2) treatment. Fertilizer additions frequently result in enhanced N_2O loss pathways (Robertson et al., 2012). It is notable, however, that the N_2O emissions in the intercrop treatment were essentially the same as the unfertilized IWG(2) even though the difference in cumulative N balances between these two treatments was >300 kg ha^{-1} in both years 3 and 4 (**Figure 4B**). We predict that N_2O emissions from perennial legume-cereal intercrops that are closer to equilibrium with respect to soil organic matter may be greater than those emitted in agroecosystems actively aggrading SOM. Even if N_2O emissions are found to increase some in an intercrop that is less limited by N, the improved synchrony demonstrated in this diverse, perennial agroecosystem may be a viable ecological nutrient management strategy for reducing N_2O emissions.

Future Research Directions

While the IWG-ALF intercrop may have several promising attributes worth considering in future intercrop designs, the insufficient N asynchrony that appears to have limited intercrop productivity compared to fertilized monocrops in years 1–3 deserves attention. As demonstrated in this study, substantial inputs of N through BNF and yet only a small fraction of these inputs became available to IWG. Nevertheless, results here suggest that small improvements in N availability may significantly improve yields. This will be increasingly important as the yield potential of IWG continues to increase through intensive breeding efforts (Crain et al., 2021a,b). We propose several design or management innovations that have the potential to relax intercrop N limitation in the first years following stand establishment.

1. **Add clover to alfalfa to improve N synchrony**. Alfalfa is widely recognized for maintaining very high rates of N fixation over many years, and has deep tap roots that may facilitate water resource partitioning with IWG and other cereals (Thilakarathna et al., 2016b; Corentin et al., 2022). However, compared to white and red clovers, a much lower percentage of alfalfa fixed-N becomes available to intercropped species within a 1–2 year timeframe (Louarn et al., 2015; Thilakarathna et al., 2016b). By diversifying the legume component of the intercrop, such as co-sowing red clover and alfalfa with IWG, it may be possible to take advantage of more rapid cycling N from clover, while benefiting from the slower N build-up and subsequent N mineralization that we saw in this study with alfalfa after 2015.
2. **Add modest N amendments in years 1–2 to improve N synchrony**. In a recent pot experiment in which IWG was intercropped with white clover in different plant density ratios and N fertilization regimes, Li et al. (2021) reported how the %Ndfa of clover was 60% when an IWG-clover intercrop was fertilized with the equivalent of 225 kg N ha^{-1}. This relatively high %Ndfa in the face of large N inputs suggests that IWG is able to take up most mineral N in the soil avoiding suppression of N fixation. If this result is transferable to the field, then it may be possible to fertilize an IWG-ALF intercrop with manure, urine, or synthetic fertilizer while still benefitting from alfalfa N fixation and accumulation.
3. **Improve synchrony with a "rotational intercrop."** Given the 2–3 year lag shown in this study between the onset of alfalfa N fixation inputs and adequate levels of net N mineralization to IWG in the intercrop, we suggest a cropping system that combines elements of a rotation and an intercrop to enhance N synchrony. The design involves planting and harvesting forage from a solid stand of alfalfa, effectively frontloading organically-bound N into the soil. After 2 or 3 years, terminate strips of alfalfa using an undercutter implement or herbicides, and sow intermediate wheatgrass, while leaving strips of living alfalfa intact. In this design, newly established wheatgrass could take advantage of a potentially elevated rates of N mineralization resulting from alfalfa termination, while also benefitting from ongoing N inputs from living, intercropped alfalfa.

CONCLUSIONS

This study is one of the first involving a detailed evaluation of how the N economy of a perennial cereal-legume intercrop functions with respect to sustaining productivity and improving on ecosystem services. Relative to unfertilized IWG treatments, IWG grain and biomass yields showed clear evidence of net facilitation by alfalfa after the establishment year. However, comparisons with fertilized and unfertilized IWG monocrops suggested that N inputs from alfalfa N fixation gradually relax but do not eliminate N limitation in the intercrop. In spite of N limitation, the intercrop was the only treatment that did not experience significant declines in IWG grain yields over the 5-year experiment. Estimated cumulative N inputs from alfalfa

N fixation in the intercrop substantially exceeded N exports in grain and biomass, suggesting a legacy of good soil fertility for the crop following the IWG-ALF intercrop. Intercropping IWG with alfalfa had the surprising effect of almost doubling root biomass in surface horizons, and the synchrony of N supply and demand appeared to be high as N_2O emissions in the intercrop were similar to the unfertilized IWG monocrop and significantly lower than the fertilized monocrop. Taken as a whole, the IWG-alfalfa intercrop encompasses a wide range of ecological nutrient management functions—reliance on legume BNF, improvement in N fertility as a consequence of cropping, reduced N_2O emissions, and potential to increase SOM with greater root biomass. Research to bolster N availability in the early years of the intercrop, while alfalfa builds soil organic nitrogen for sustaining later years of productivity would be worthwhile.

We believe these findings will be useful as work continues to expand opportunities for ecological nutrient management in the ongoing effort to achieve zero hunger. In the near-term, IWG along with other perennial grains undergoing *de novo* domestication will most meaningfully contribute to food production through dual use management in which grain yields compliment forage for livestock (Ryan et al., 2018). Perennial grains can also be integrated into rotations with annual crops, enhancing yields and other services through ecological intensification of entire cropping systems (Ryan et al., 2018). Both the dual-use and rotation near term uses of perennial grains will be significantly enhanced by intercropping with a perennial legume. As investments and intensive breeding efforts continue to expand and improve on perennial grain yields, yield stability and other traits, this new crop "hardware" is expected to provide novel opportunities for increasing food security while improving soil health and contributing to climate change mitigation and adaptation (Crews et al., 2018).

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

EM conducted mixed linear model statistical analyses, as well as all statistical analyses of nitrous oxide emissions. LK, JB, and TC maintained and sampled the field experiment and carried out laboratory analyses. TC was lead author on the article, but all authors contributed to it and approved the final version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.755548/full#supplementary-material

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Advancing the science and practice of ecological nutrient management for smallholder farmers

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Soil degradation is widespread in smallholder agrarian communities across the globe where limited resource farmers struggle to overcome poverty and malnutrition. This review lays out the scientific basis and practical management options for an ecologically based approach to sustainably managing soil fertility, with particular attention to smallholder subsistence systems. We seek to change the trajectory of development programs that continue to promote inorganic fertilizers and other high input strategies to resource constrained smallholders, despite ample evidence that this approach is falling short of food security goals and contributing to resource degradation. Ecological nutrient management (ENM) is an agroecological approach to managing the biogeochemical cycles that govern soil ecosystem services and soil fertility. The portfolio of ENM strategies extends beyond reliance on inorganic fertilizers and is guided by the following five principles: (1) Build soil organic matter and other nutrient reserves. (2) Minimize the size of N and P pools that are the most susceptible to loss. (3) Maximize agroecosystem capacity to use soluble, inorganic N and P. (4) Use functional and phylogenetic biodiversity to minimize bare fallows and maximize presence of growing plants. (5) Construct agroecosystem and field scale mass balances to track net nutrient flows over multiple growing seasons. Strategic increases in spatial and temporal plant species diversity is a core ENM tactic that expands agroecosystem multifunctionality to meet smallholder priorities beyond soil restoration and crop yields. Examples of ENM practices include the use of functionally designed polycultures, diversified rotations, reduced fallow periods, increased reliance on legumes, integrated crop-livestock production, and use of variety of soil amendments. These practices foster soil organic matter accrual and restoration of soil function, both of which underpin agroecosystem resilience. When ENM is first implemented, short-term yield outcomes are variable; however, over the long-term, management systems that employ ENM can increase yields, yield stability, profitability and food security. ENM rests on a

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solid foundation of ecosystem and biogeochemical science, and despite the many barriers imposed by current agricultural policies, successful ENM systems are being promoted by some development actors and used by smallholder farmers, with promising results.

KEYWORDS

agricultural diversification, soil organic matter, nutrient use efficiency, nutrient cycling, decomposition, agroecology, biological N fixation, soil restoration

Introduction

Smallholder subsistence farming systems provide food to almost half the global human population. Limited access to resources makes it challenging for farmers to replenish soil nutrient reserves and compensate for harvested removals, leading to soil organic matter[1] (hereafter, SOM) depletion and soil erosion (Tittonell and Giller, 2013; Tully et al., 2015; Barbier and Hochard, 2018). Time lags exacerbate the downward trend in soil fertility because management is oriented toward annual food production, whereas soil degradation accrues over decadal timescales. As soil fertility and yields decline, smallholders often respond by intensifying cropping systems in ways that undermine soil fertility and food security, creating a downward spiral of malnutrition and poverty (Vanek et al., 2016; Barbier and Hochard, 2018).

Ecological nutrient management (hereafter, ENM) is a comprehensive, ecologically based approach to sustaining soil fertility (Drinkwater and Snapp, 2007a; Drinkwater et al., 2017). Ecological nutrient management aims to restore and maintain SOM/nutrient reservoirs, achieve acceptable yields, balance nutrient additions with exports, and minimize nutrient/soil losses. Our initial paper introduced ENM and focused on how this approach could reduce environmental nutrient losses in high-input, industrial farming systems (Drinkwater and Snapp, 2007a). Here, we shift our emphasis to smallholder farming systems where nutrient mining and degraded soils are pervasive. We first present the guiding principles of ENM and highlight features which distinguish ENM from conventional nutrient management. We then review the current understanding of SOM pools and their functions incorporating new understanding of the mechanisms regulating SOM dynamics and discuss the roles of plants and decomposers in governing elemental cycling processes. Then we discuss how ENM creates positive feedbacks that increase agroecosystem adaptive capacity and resilience and discuss core management strategies using three case studies of ENM in smallholder systems in Sub-Saharan Africa. Lastly, we briefly examine the obstacles that privilege the use of synthetic fertilizers while discouraging implementation of ENM strategies and present ideas about how these barriers can be overcome.

How does ENM differ from conventional nutrient management?

Conventional nutrient management aims to maximize inorganic fertilizer (F_i) use efficiency by reducing temporal asynchrony and spatial separation between F_i applications and crop uptake (Table 1; Cassman et al., 2002). To achieve this goal, a collection of best management practices designated as "4Rs Nutrient Management" (4R-NM) is widely promoted. The 4R-NM system seeks to maximize crop uptake of F_i using "the Right F_i source, at the Right rate, at the Right time, with the Right placement" (Vollmer-Sanders et al., 2016; Fixen, 2020). Compared to earlier strategies that often focused on one aspect of F_i management, 4R-NM is more comprehensive; however, the focus is still on a single growing season, and 4R-NM does not attempt to manage SOM reserves or the long-term trajectory of SOM levels. Thus, crop yield improvements can be rapidly apparent under 4R-NM due to high doses of F_i or "rescue" F_i applications, while the slower process of SOM decline continue (Ladha et al., 2011). Over the long-term, simplified rotations of crops bred to be highly responsive to F_i combined with SOM declines and diminished nutrient recycling act together to reinforce F_i dependency. This creates what has been termed a fertilizer treadmill (Drinkwater and Snapp, 2007a,b; Houser and Stuart, 2020).

ENM extends an ecological conceptual framework to agricultural management (Table 1). The nitrogen (N) saturation hypothesis was developed to explain changes in forest ecosystem biogeochemistry resulting from chronic anthropogenic N deposition and provides the theoretical foundation for ENM (Agren and Bosatta, 1988; Aber et al., 1989). According to this hypothesis, ecosystems are N saturated when primary productivity is no longer limited by N, and N additions exceed the capacity of the ecosystem to cycle or store N internally. Nitrogen flows are governed largely biotic processes, so retention of N depends on plant and microbial assimilation while microbial N transformations (nitrification/denitrification)

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[1] Refers to soil organic matter in its entirety including all elements.

TABLE 1 Management strategies employed, and pools/processes targeted by 4R-NM and ENM.

4Rs F_i management	Ecological nutrient management
Nutrient supply	
- Primarily soluble, inorganic fertilizers (F_i)	- Reliance on BNF and strategic use of diverse nutrient sources
- Optimize delivery of F_i: Right rate, form, time, and placement	- Maintain reservoirs with longer MRTs that can be accessed by plants and microbes
- Use soil tests to predict plant available P and net N mineralization; match F_i applications accordingly	- Promote exchanges of C from plants for N and P released by decomposers
Actively managed soil pools	
- Inorganic N, extractable P	- All N and P pools, organic and inorganic
Plant management strategies	
- Manage crop to create a strong sink for F_i	- Use of plant diversity to maximize N and P assimilation
- Remove all crop growth limiting factors	- Select species to provide diverse belowground ecosystem services
Microbial and abiotic transformations	
- Chemical additives to inhibit nitrification and denitrification	- Reduce the size of soluble N_i and P_i
- Reduce surface area of fertilizer patches	- Promote microbial uptake and growth
- Optimize pH to reduce P-fixation	- Promote plant-mediated microbial transformations that supply nutrients

Modified from Drinkwater and Snapp, 2007a. BNF, biological N fixation; MRT, mean residence time.

drive N losses from ecosystems. More recently, the N saturation conceptual framework has been extended to P (Deng et al., 2017; Chen et al., 2021) with some modifications due to differences in N and P cycles. While N sinks and transformations are primarily controlled by plant- and microbially-mediated processes, P cycling processes include several abiotic mechanisms, including precipitation-dissolution, sorption-desorption, and occlusion. These geochemically mediated sinks compete with biological assimilation for the small amounts of soluble, inorganic P (hereafter P_i) which are typically present in the soil solution (Attiwill and Adams, 1993). Under P saturation, excess soluble P can be captured by geochemical processes ("fixed") essentially removing P from the biological P cycle.

There are two key aspects of this ecosystem-based framework that inform ENM. First is the recognition that time lags and cycling processes occurring across spatial/temporal scales influence ecosystem-scale accrual or loss of carbon (C), N and phosphorus (P). Second, the framework highlights the importance of interactions among elemental cycles and clarifies the role of C-N-P coupling in determining whether conservation or loss pathways dominate.

Thus, the overarching goal of ENM is to manage agroecosystems to reach dynamic steady states where SOM formation equals decomposition, nutrient additions equal harvested exports, and yields and SOM/nutrient reserves are maintained. The scope of ENM extends beyond promoting fast, single season nutrient supply to consider all processes governing biogeochemical cycling across spatial and temporal scales (Figure 1). ENM aims to recouple elemental cycling processes at multiple temporal and spatial scales to restore soil nutrient reserves that can be accessed by plants. As a result, the ENM portfolio includes a diverse array of management practices that seek to recouple elemental cycles, promote conservation pathways and gradually rebuild SOM and regenerate biogeochemical resilience (Drinkwater and Snapp, 2007a).

Guiding principles of ENM

1. **Build SOM and other nutrient reserves**. Because plants can access many forms of N and P though partnerships with beneficial microorganisms living in the rhizosphere, ENM targets the full range of nutrient reservoirs. The basic strategy is to conserve and build nutrient reserves that are less vulnerable to loss which can be accessed through rhizosphere and microbially mediated processes. These reserves include labile and stabilized SOM, microbial biomass, and sparingly soluble plus some forms of adsorbed P.
2. **Minimize the size of N and P pools that are the most susceptible to loss**. A central objective of ENM is to reduce loss pathways by minimizing standing pools of soluble inorganic N (hereafter, N_i) and P_i in soil, fostering plant and microbial assimilation, and reducing N_i and P_i additions. While the loss mechanisms differ, greater concentrations of N_i and P_i promote nutrient losses. As the concentration of N_i increases, leaching and denitrification increase. Phosphorus is less mobile, but most soils, particularly highly weathered soils commonly found in the Global South, "fix" excess soluble P though adsorption, precipitation, and occlusion. Reducing F_i rates is a powerful lever for significantly reducing N_i and P_i losses.
3. **Maximize agroecosystem capacity to use soluble, N_i and P_i**. Plant and microbial acquisition increase internal

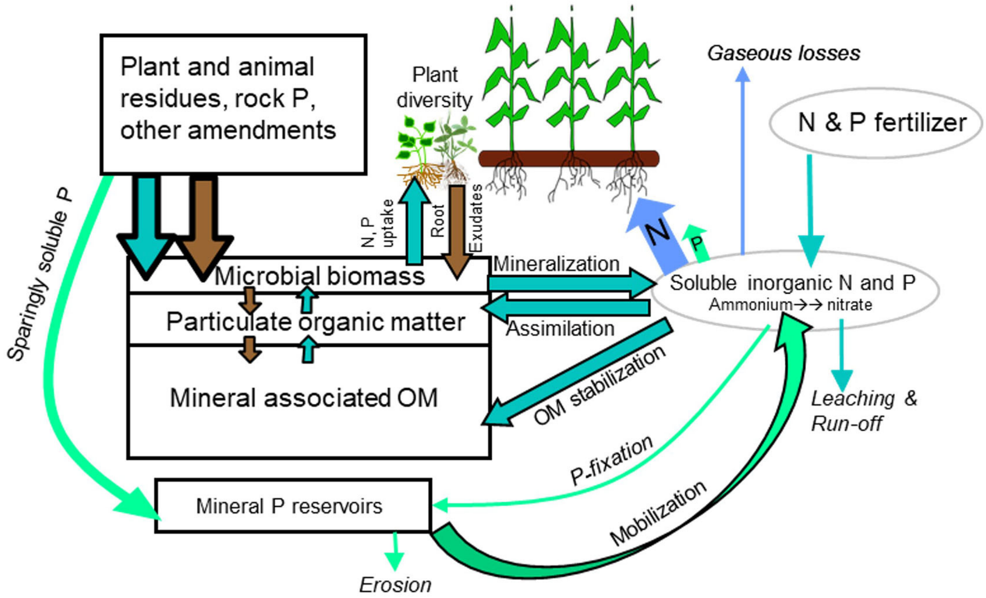


FIGURE 1
ENM expands the focus of nutrient management to SOM pools and mineral P reserves. Flows, inputs, and pools that are increased under ENM are outlined in black. Arrow colors indicate dominant elemental fluxes as follows: N only (blue), P only (green), N and P (blue green), and C (brown). Modified after Drinkwater and Snapp, 2007a.

cycling, removing soluble nutrients from the soil solution, preventing their loss from the soil, and diverting N_i and P_i flows into SOM reserves. The greater abundance of soil C relative to N_i and P_i fuels the growth of soil organisms, increasing SOM formation.

4. **Use functional and phylogenetic biodiversity to minimize bare fallows and maximize presence of growing plants**. Plant and microbial species differ in their capacity to carry out elemental cycling processes. Diversifying crop rotations and reducing use of bare fallows by adding cover crops or perennials in conjunction with legume N sources are effective strategies for recoupling elemental cycles (Figure 1). Using plant diversity to maximize niche occupancy and promote a more functionally diverse soil biota can enhance overall productivity and nutrient cycling capacity of belowground communities. Integrated crop-livestock farming systems expand opportunities for diversification of plants and implementation of ENM.
5. **Construct agroecosystem and field scale mass balances to track net nutrient flows over multiple growing seasons**. Using simple mass balances ensures that soil mining, where crop harvests remove greater amounts of N and P compared to additions, can be detected, and addressed. Long-term removal of nutrients that exceeds nutrient additions undermines soil fertility and leads to soil degradation. This is the situation in many smallholder subsistence systems. On the other end of the spectrum, limiting the degree to which nutrient additions exceed harvested removals reduces the risk of environmental losses.

Ecosystem processes that govern C, N and P cycling

Successful application of ENM principles is grounded in a basic understanding of the biological and geochemical processes governing soil elemental cycles. Ecosystem state factors (climate, parent material, topography, potential biota, time, and human activities) are the master regulators of SOM levels (Jenny, 1941). The legacy of these factors provides the context for agricultural management to affect elemental cycles and SOM reserves (Amundson and Jenny, 1997; Kleber et al., 2015). Thus, the environmental context, management history and the current management regime determine the balance between decomposition and SOM formation/ stabilization. Over the past decade, major discoveries have fundamentally altered our understanding of SOM biogeochemistry (Kuzyakov and Xu, 2013; Lavallee et al., 2020; Liang et al., 2020; Daly et al., 2021).

The fundamentally distinct components of SOM

The diverse functions of SOM reflect the heterogeneous composition of SOM reserves (Figure 2). Specifically, SOM pools differ in terms of turnover rate, nutrient density, the degree

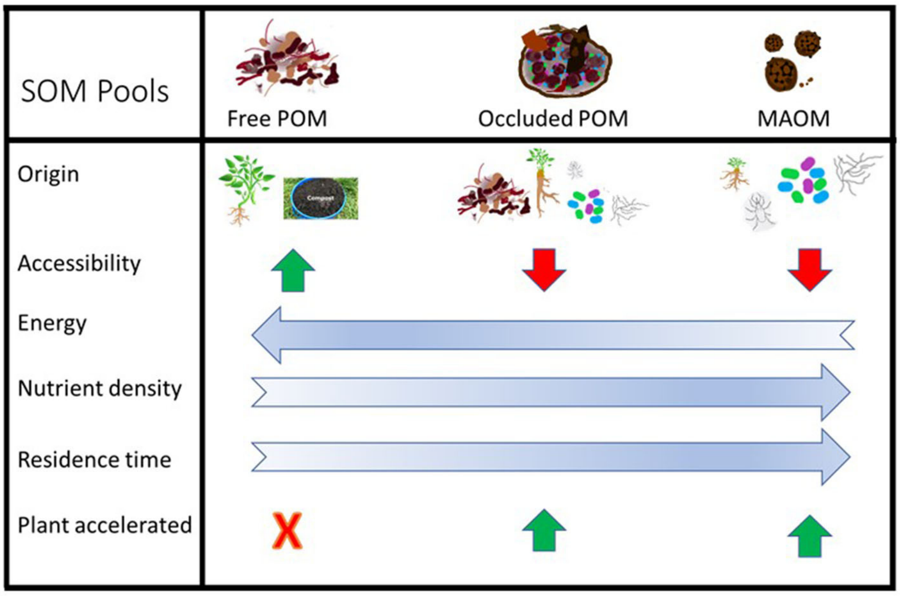


FIGURE 2
Soil OM pools differ in composition and function. Compared to occluded particulate OM (POM) and mineral associated OM (MAOM), free POM is more accessible to decomposers, more energy rich but nutrient poor with a relatively fast turnover time (Liang et al., 2019; Lavallee et al., 2020). Occluded POM and MAOM are protected through their association with mineral constituents, and while they are nutrient rich, C limitation may also hinder decomposer access. As a result, plant driven priming of decomposition is most pronounced for oPOM and MAOM (Daly et al., 2021).

to which they are associated with mineral elements and their response to management practices (Lehmann and Kleber, 2015; Williams et al., 2018; Sokol et al., 2022). These distinct SOM reserves act together to support soil ecosystem integrity and plant growth.

Most SOM is present as mineral associated organic matter (MAOM) which has turnover times ranging from decades to millennia. MAOM accounts for >90% of soil organic C (hereafter, C_{org}, refers to elemental C content of SOM) and plays a significant role in C_{org} sequestration, nutrient supply to plants and decomposers, and stabilization of small aggregates (Kleber et al., 2015). It is largely composed of microbial-derived monomers and polymers produced during decomposition and stabilized through protective associations with mineral components (von Lutzow et al., 2006; Schmidt et al., 2011; Liang et al., 2019). Rhizodeposition, litter composition, microbial C use efficiency, and soil mineralogy, all govern MAOM accrual (Puget and Drinkwater, 2001; Kallenbach et al., 2015; Lavallee et al., 2018). Interactions with minerals limit decomposer access to MAOM constituents, however, MAOM can still be accessed by decomposers and, as a result, decomposition of MAOM can dominate cycling of micro- and macro-nutrients due to the sheer size of this reserve (Lavallee et al., 2020).

Particulate organic matter (POM), defined as OM particles $\geq$53 um, is less abundant than MAOM but far more dynamic. POM consists of plant litter and microbial residues in varying stages of decay and is divided into two distinct pools that are either free from mineral interactions (free POM, hereafter fPOM), or are protected by soil minerals, usually by occlusion inside of aggregates (occluded POM, hereafter oPOM). Compared to MAOM, these labile pools which have shorter turnover times are more sensitive to management changes and accumulate C and N more quickly (Wander et al., 1994; John et al., 2005; Lavallee et al., 2020). Free POM is the raw material that is transformed into oPOM and MAOM during decomposition (Puget and Drinkwater, 2001).

While fPOM acts primarily as a food source for decomposers, oPOM contributes to a broader array of soil functions. Compared to fPOM, oPOM has a narrower C:N ratio, serves as an important source of mineralizable N and plays a significant role in aggregate stability (von Lutzow et al., 2006; Bu et al., 2015). Accordingly, increases in nutrient rich oPOM stocks contribute to soil fertility while also improving soil structural properties dependent on soil aggregation. These processes of organic N and P (hereafter N_{org} and P_{org} refer to organic forms of these elements) storage and soil aggregation in turn support plant nutrient acquisition and improve agroecosystem resiliency to extreme variation in precipitation. The sensitivity of oPOM to management changes, combined with its central role in key soil functions, makes oPOM particularly useful as an early indicator of the trajectory of SOM levels and soil health (Wander et al., 1994; Schmidt et al., 2011).

The role of plants in promoting decomposition and SOM formation

The rhizosphere is a site of plant-microbial interactions and compared to bulk soil, microbial metabolism in the rhizosphere is an order of magnitude greater due to root exudates that support microbial growth (Philippot et al., 2009). Labile exudates and other rhizodeposits alleviate energetic constraints on microbial extracellular enzyme production (Averill and Finzi, 2011; Dijkstra et al., 2013), leading to mineralization of nutrient-rich SOM (Hamilton and Frank, 2001; Weintraub et al., 2007; Kuzyakov, 2010). By supplying amino acids, sugars and other organic compounds, plants can cultivate distinct communities of microbes that facilitate decomposition of nutrient rich SOM reserves which can in turn increase the amount of N and P available to plants (Reynolds et al., 2003; Panke-Buisse et al., 2015; Jilling et al., 2018; Dijkstra et al., 2021). The significance of this process is supported by field studies where despite substantial F_i additions, N_{org} reserves supply a majority of grain crop N (Gardner and Drinkwater, 2009; Yan et al., 2020). The stimulation of decomposition spurs microbial growth and turnover promoting SOM formation and soil aggregation (Alami et al., 2000; Atkinson and Urwin, 2012). Thus, these plant-microbial interactions occurring in the rhizosphere contribute to the disproportionate accrual of root-derived C into oPOM and MAOM (Fulton-Smith and Cotrufo, 2019; Sokol et al., 2019a).

Greater species richness and increased plant functional diversity go together, expanding the influence of plants on a wide range of belowground processes (Cadotte et al., 2011; Cardinale et al., 2011). Examples of key plant functional traits include life history and nutrient acquisition strategies, the quantity/composition of litter and rhizodeposits, and root turnover rate (Haynes and Beare, 1997; Bardgett et al., 2014; Li et al., 2014; Poirier et al., 2018). Rhizosphere microbiome composition and function vary with plant species/cultivar and are linked to plant ecological niche and nutrient requirements (Peiffer et al., 2013; Turner et al., 2013; Emmett et al., 2017). Plant-microbial partnerships jointly control processes such as aggregate formation, N cycling dynamics and the net balance between SOM decomposition and formation in the rhizosphere (Figure 3; Briones et al., 2003; Philippot et al., 2013; Emmett et al., 2020). For example, fast growing plant species, including crops such as maize, tend to be net mineralizers and accelerate decomposition and N cycling rates (Castro-Diez et al., 2014). In contrast, many legume species build SOM because the rate

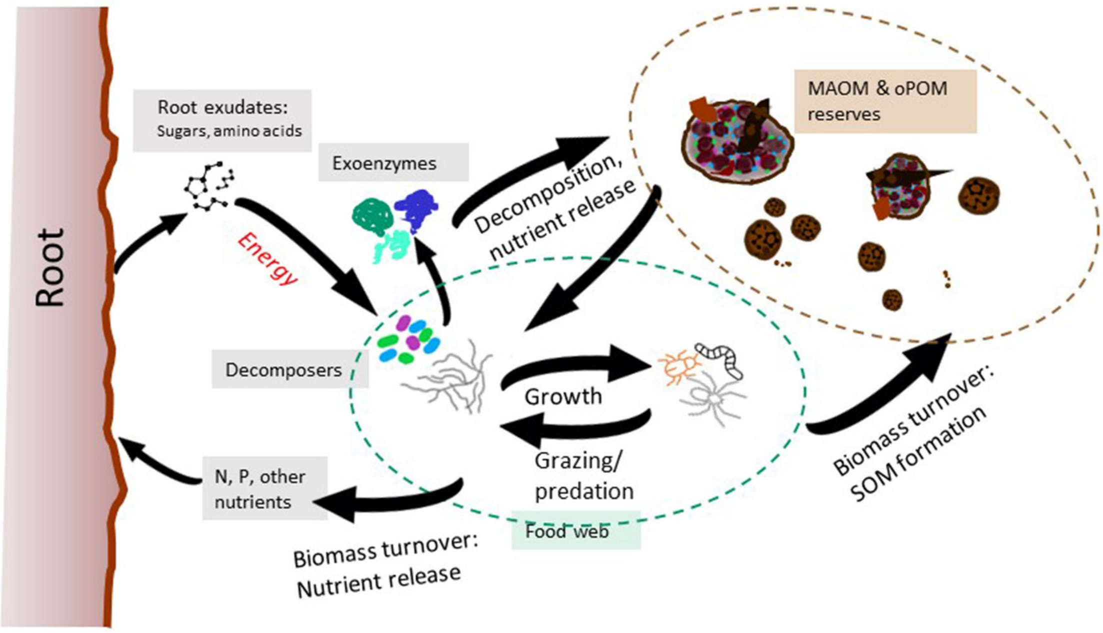


FIGURE 3
In the rhizosphere, decomposition and stabilization/formation of SOM occur simultaneously. Plants exchange C substrates for nutrients released by the decomposers. Organic compounds and ions are secreted by plant roots into the rhizosphere providing energy to decomposers and enabling them to produce expensive exoenzymes needed to access nutrient rich oPOM and MAOM fueling microbial growth. The resulting microbial biomass supports grazers and predators, and these trophic interactions release N and P that can then be taken up by roots. Growth and turnover of decomposers and soil food web organisms increases the flow of necromass and replenishes oPOM and MAOM reserves. Modified after Liang et al., 2017 and Valadares et al., 2020.

of oPOM and MAOM formation in the rhizosphere exceeds decomposition (Puget and Drinkwater, 2001; Garland et al., 2018).

Microbial control of SOM dynamics

While all SOM originates from plant inputs and other organic residues (e.g., manures, composts), the bulk of stabilized SOM is composed of microbial biomass or "necromass" (Liang et al., 2017). In the same way that plant species effects on elemental cycling processes depend on life history strategies and corresponding plant functional traits, decomposers differ in their impact on C, N and P cycling processes. Microbial C use efficiency (hereafter CUE), is defined as the proportion of organic C taken up that is allocated to microbial growth (Kallenbach et al., 2019). Life history strategy determines the ecological and physiological characteristics that govern microbial allocation of energy to growth, resource acquisition, respiration, and survival (Roller et al., 2016; Malik et al., 2020). Microbial CUE ultimately determines the efficiency of microbial conversion of plant-derived C into stabilized, nutrient rich SOM reserves (Kallenbach et al., 2015; Barnett et al., 2021). Thus, the growth dynamics of soil microorganisms are another determinant of SOM accrual (Caruso et al., 2018; Sokol et al., 2019b).

Ecological nutrient management: Many little hammers

Liebman and Gallandt (1997) used the phrase "many little hammers" to describe the benefits of orchestrating many practices to achieve effective weed control without the use of herbicides. This view captures the fundamental nature of all agroecological management strategies, including ENM. To achieve the short-term goals of a single growing season while being mindful of the trajectory of slower processes requires coordinated use of multiple practices while also recognizing that each practice can affect many cycling processes. Ultimately, shifts in fast cycling processes, the resulting changes in slower processes, and the ensuing feedbacks favoring conservation pathways increase the capacity of agroecosystems to supply crop nutrients (Drinkwater and Snapp, 2007a). Tolerance to stressors can also improve over the long-term as SOM accrual alters the soil environment and the soil community undergoes changes in composition (Petersen-Rockney et al., 2021). Here we first elaborate on interactions among fast and slow processes and highlight resulting feedbacks that promote soil restoration. We then discuss four core management strategies, focusing on practices that are likely to be most compatible with smallholder farming systems: (1) Diversification of plant species, (2) Inclusion of legumes and perennials, (3) Crop-livestock integration and (4) Nutrient sources and soil amendments.

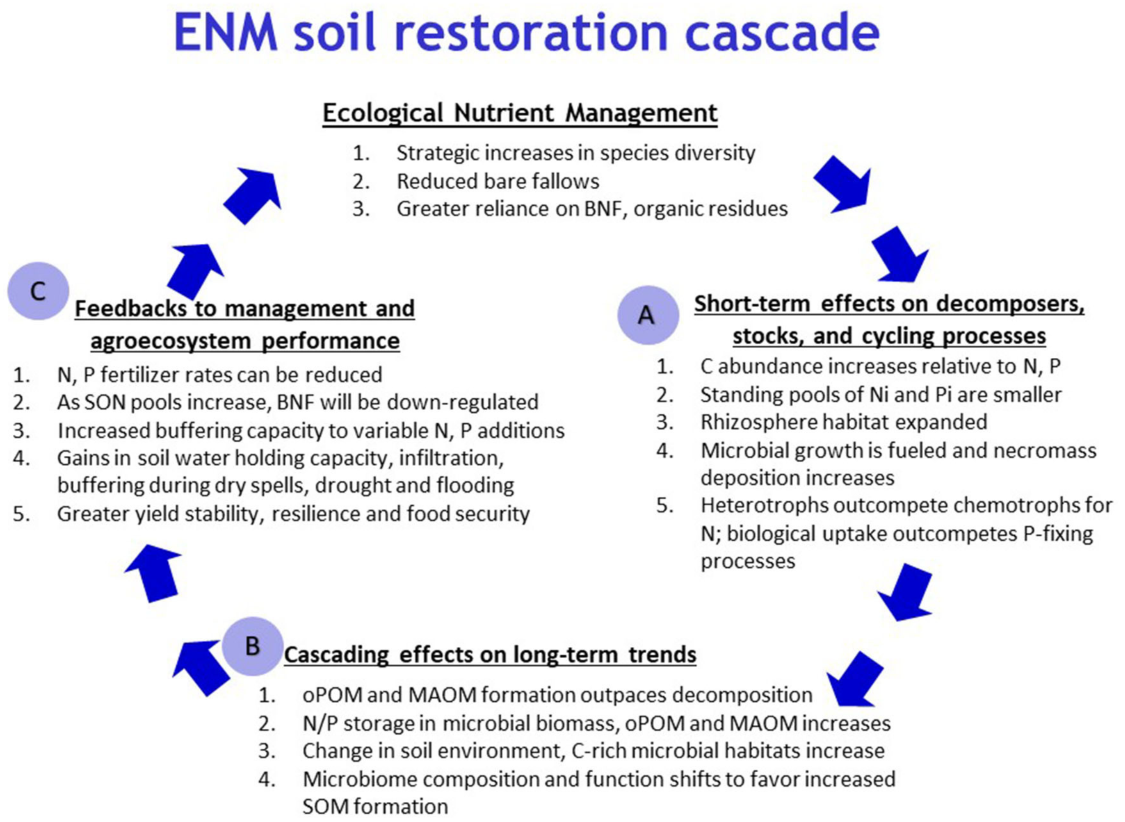
ENM and the soil restoration cascade

There are two distinct types of feedbacks governing the positive cycle of soil restoration under ENM (Figure 4). Reinforcing (positive) feedbacks amplify change and result in transitions to different steady states. An example of a reinforcing feedback loop is the effect of management practices that increase C_{org} levels which in turn impact soil microbiome composition and function. Greater C abundance relative to N_i and P_i increases microbial growth and the flow of necromass derived C, N and P into SOM reserves. Greater SOM levels favor microbial communities that channel C into growth over maintenance favoring SOM accrual (McDaniel et al., 2014; Kallenbach et al., 2015; Buckeridge et al., 2020). Stablilizing (negative) feedbacks slow processes and favor dynamic steady states and greater stability. Downregulation of biological N fixation in legumes in response to increases in soil N supply capacity is an example of a stabilizing feedback loop. Greater reliance on legumes to supply N increases oPOM N reserves and soil N supply capacity resulting in legume downregulation of N_2 fixation and reduces legume N additions and the potential for N surpluses and N losses over the long-term (Blesh and Drinkwater, 2013; Blesh, 2019).

Under ENM, key shifts in elemental cycling, soil environmental conditions and C/N/P stocks in the short term (Figure 4A) set the stage for conservation pathways and changes in microbial community composition and function (Figure 4B) creating reinforcing feedbacks that tighten nutrient cycles and increase soil fertility leading to improved crop yields, yield stability, and permit further management adjustments (Figure 4C). Soils cannot accrue unlimited SOM or nutrient stocks, so ultimately a new steady state condition is reached. Ecosystem state factors (e.g., climate, soil texture/parent material) and management determine these limits to SOM accrual and the extent of soil restoration that can be achieved under ENM regimes.

Plant species diversity

ENM cannot be effectively implemented without strategic increases in spatial and temporal plant species diversity. Polycultures (intercropping and agroforestry), diversified rotations, and cover cropping are diversification practices used by farmers to improve yields (Figure 5). In polycultures, beneficial plant-plant interactions, including complementarity, resource partitioning and facilitation increase nutrient acquisition and improve fertilizer and water use efficiency (Iverson et al., 2014; Brooker et al., 2015; Duchene et al., 2017).



ENM soil restoration cascade

Ecological Nutrient Management

1. Strategic increases in species diversity
2. Reduced bare fallows
3. Greater reliance on BNF, organic residues

A **Short-term effects on decomposers, stocks, and cycling processes**

1. C abundance increases relative to N, P
2. Standing pools of Ni and Pi are smaller
3. Rhizosphere habitat expanded
4. Microbial growth is fueled and necromass deposition increases
5. Heterotrophs outcompete chemotrophs for N; biological uptake outcompetes P-fixing processes

B **Cascading effects on long-term trends**

1. oPOM and MAOM formation outpaces decomposition
2. N/P storage in microbial biomass, oPOM and MAOM increases
3. Change in soil environment, C-rich microbial habitats increase
4. Microbiome composition and function shifts to favor increased SOM formation

C **Feedbacks to management and agroecosystem performance**

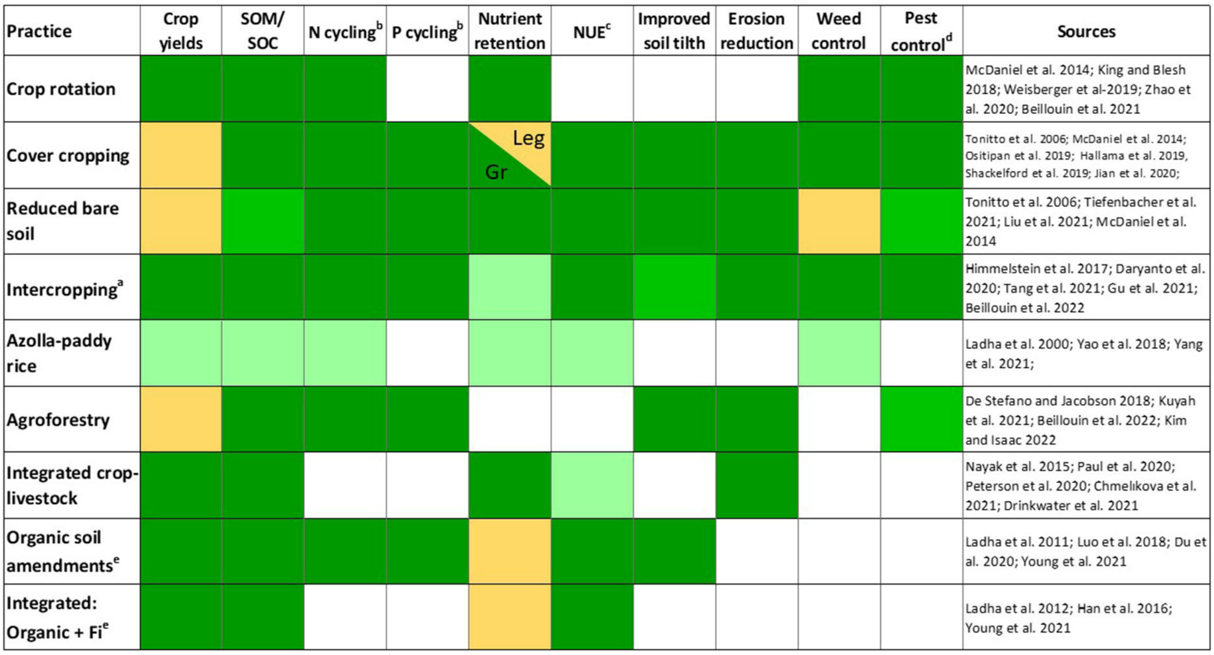
1. N, P fertilizer rates can be reduced
2. As SON pools increase, BNF will be down-regulated
3. Increased buffering capacity to variable N, P additions
4. Gains in soil water holding capacity, infiltration, buffering during dry spells, drought and flooding
5. Greater yield stability, resilience and food security

FIGURE 4
ENM shifts soil processes to favor a positive trajectory of SOM accrual and soil restoration. The diagram depicts changes resulting from implementation of ENM in a degraded soil with a history of inadequate F_i additions and meager returns of senescent crop residues, a situation commonly found in limited resource, smallholder systems. In the short term, cycling processes and microbial communities are altered to favor conservation pathways **(A)** which have cascading effects on SOM accrual, nutrient retention, and microbial community composition/function **(B)** and lead to feedbacks that ultimately impact yields, yield stability/resilience and management **(C)**. BNF, biological N fixation.

Likewise, diversification of annual rotations by adding species with complementary phenology to minimize bare fallows, increases nutrient retention and promotes SOM accrual (Blesh, 2019; Hallama et al., 2019; Blanco-Canqui and Ruis, 2020; Kim et al., 2020; Beillouin et al., 2021). Maximizing belowground ecosystem services requires attention to the ecological niche and the capacity of functional groups or species to promote desirable processes. For example, while all legumes can fix N, there is considerable variation in rhizosphere effects on elemental cycling processes across species. *Lupinus* sp. can mobilize sparingly soluble P though rhizosphere acidification while other legume species such as *Vicia* sp. increase soil phosphatase activity and mineralization of P_{org} (Balota et al., 2014; Hallama et al., 2019). Creating polycultures through purposeful diversification with companion species offers the greatest potential to maximize complex belowground ecosystem services. In paddy rice systems, use of Azolla as a companion intercrop increases N use efficiency, reduces N losses and can provide yield benefits (Yao et al., 2018; Yang et al., 2021). Other examples are discussed in the case studies below.

Inclusion of perennials and legumes

Among the immense diversity of plants, legumes and perennial species stand out because of their exceptional capacity to expedite SOM formation/stabilization, N and P recycling efficiency, and soil restoration. Reliance on biological N fixation reduces F_i dependance and as the proportion of legume derived N increases, agroecosystem-scale N use efficiency increases, reducing the potential for environmental N losses (Blesh and Drinkwater, 2013; Blesh, 2019). Diversification with legumes can mobilize mineral P reserves and promote accrual of SOM increasing N_{org}/P_{org} stocks that are accessible to cash crops (Hallama et al., 2019; Jian et al., 2020). Furthermore, compared to annuals, perennials have a greater capacity to restore soil functions and SOM reserves (Crews et al., 2016; Crews and Rumsey, 2017). Compared to cropping systems composed of annuals, adding perennial forage species to rotations or as intercrops promotes soil restoration through reduced erosion, SOM/N_{org}/P_{org} accrual, and aggregate formation (Garland et al., 2018; Paul et al., 2020; Drinkwater et al., 2021). In



Practice	Crop yields	SOM/ SOC	N cycling[b]	P cycling[b]	Nutrient retention	NUE[c]	Improved soil tilth	Erosion reduction	Weed control	Pest control[d]	Sources
Crop rotation	🟩	🟩	🟩		🟩				🟩	🟩	McDaniel et al. 2014; King and Blesh 2018; Weisberger et al-2019; Zhao et al. 2020; Beillouin et al. 2021
Cover cropping	🟧	🟩	🟩	🟩	Leg 🟧 Gr 🟩	🟩	🟩	🟩	🟩	🟩	Tonitto et al. 2006; McDaniel et al. 2014; Ositipan et al. 2019; Hallama et al. 2019, Shackelford et al. 2019; Jian et al. 2020;
Reduced bare soil	🟧	▩	🟩	🟩	🟩	🟩	🟩	🟩	🟧	▩	Tonitto et al. 2006; Tiefenbacher et al. 2021; Liu et al. 2021; McDaniel et al. 2014
Intercropping[a]	🟩	🟩	🟩	🟩	▨	🟩	▩	🟩	🟩	🟩	Himmelstein et al. 2017; Daryanto et al. 2020; Tang et al. 2021; Gu et al. 2021; Beillouin et al. 2022
Azolla-paddy rice	▨	▨	▨		▨	▨			▨		Ladha et al. 2000; Yao et al. 2018; Yang et al. 2021;
Agroforestry	🟧	🟩	🟩	🟩			🟩	🟩		▩	De Stefano and Jacobson 2018; Kuyah et al. 2021; Beillouin et al. 2022; Kim and Isaac 2022
Integrated crop-livestock	🟩	🟩			🟩	▨		🟩			Nayak et al. 2015; Paul et al. 2020; Peterson et al. 2020; Chmelıkova et al. 2021; Drinkwater et al. 2021
Organic soil amendments[e]	🟩	🟩	🟩	🟩	🟧	🟩	🟩				Ladha et al. 2011; Luo et al. 2018; Du et al. 2020; Young et al. 2021
Integrated: Organic + Fi[e]	🟩	🟩			🟧	🟩					Ladha et al. 2012; Han et al. 2016; Young et al. 2021

FIGURE 5
ENM practices provide multiple ecosystem services. Management effects on desirable ecosystem services are indicated by color, with green indicating positive effects and orange indicating mixed or inconsistent effects. Dark green indicates the evidence is strong and reflects consistent results from multiple meta-analytical reviews while medium green indicates moderate evidence (i.e., ecosystem services that were considered in a limited number of meta-analyses). The lightest shade of green indicates limited evidence, including management effects where results are from the primary literature or a single meta-analysis. The split cell for cover cropping effects on nutrient retention indicates that the effect varies with cover crop composition; grasses (Gr) consistently increase nutrient retention while legumes (Leg) have inconsistent effects. Blank cells indicate ecosystem services for which there were insufficient data points to be included in the meta-analytical reviews. [a]Legume-grass intercrops dominate this literature; [b]Plant available and N_{org}, P_{org}; [c]NUE=Nutrient use efficiency; [d]Pathogen and herbivore control; [e]Compared to Fi only.

agroforestry and alley cropping systems, belowground benefits increase in concert with the abundance of trees included with high value cash crops such as coffee and annual food crops (Tully et al., 2012; Cristobal-Acevedo et al., 2019).

Nutrient sources and organic residues

Expansion of F_i usage as a remedy for degraded soils in smallholder systems continues to be widely promoted through government programs and development agencies (Mitchell et al., 2018). Besides the emphasis on short term outcomes such as yield improvements, the assumption is that by supplying the major limiting nutrients, yields and biomass production will be greater, and the increased crop residues will reverse soil degradation and rebuild SOM (Hickman et al., 2020; Tiefenbacher et al., 2021). Compared to organic amendments, N_i has the smallest impact on C_{org} accrual (Han et al., 2016; Luo et al., 2018). In cases where greater C_{org} is detected in F_i treatments compared to zero input controls is often due to a reduced rate of SOM loss rather than net SOM accrual (Ladha et al., 2011; Ndung'u et al., 2021; Tiefenbacher et al., 2021). Use of organic amendments, either alone or paired with F_i, accelerates SOM accrual, and provides other benefits including increases in microbial abundance/activity, including beneficials such as arbuscular mycorrhizae fungi (Figure 5; Jiang et al., 2021). While fertilizers often improve crop yields in smallholder systems, sole reliance on F_i does not provide expected yield boosts (Jayne et al., 2018) or deliver substantive soil health benefits (Ndung'u et al., 2021; Young et al., 2021). A study of over one thousand smallholder fields in Malawi is a case in point; management factors associated with soil C_{org} levels included crop diversity, weeds and organic residue incorporation, but not fertilizers (Tu et al., 2022).

In conjunction with additions of these nutrient sources, simple mass balances can be constructed using all inputs and harvested removals. To be of use, mass balances of N, P and K can be calculated for at least an entire rotation cycle to capture year to year variation in nutrient additions and removals. Simple input-output calculations do not include environmental losses, which can drive significant removals, particularly for N though biotic transformations or for P and K in erosion prone situations (Vanek and Drinkwater, 2013). Nevertheless, negative balances indicate that soil nutrients are being mined, while situations where N surpluses are large indicate vulnerability to denitrification and leaching losses (Tamagno et al., 2022).

Crop-livestock integration

The coordinated production of food crops, forages and livestock (used here to include poultry/fish/edible invertebrates) can improve family nutrition, food security and income and are the backbone of many smallholder farming systems (Lindahl et al., 2020; Paul et al., 2020; Bezner-Kerr et al., 2021). Integrated crop-livestock systems encompass all these core ENM strategies and are highly compatible with ENM because the pairing of livestock with arable food crops enables farmers to include perennial species, particularly perennial legumes either through intercropping with annual food crops or alternating pastures/forage production with annual food crops in rotation. Likewise in paddy rice production, production of poultry, fish or edible crustaceans is highly compatible with use of Azolla green manures (Sivakumar and Solaimalai, 2003; Chen et al., 2017). Compared to annual grain production systems, integrated crop-livestock systems build SOM, including oPOM and MAOM and conserve nutrients through recycling (Nayak et al., 2015; Chmelikova et al., 2021; Rui et al., 2022). In Sub-Saharan Africa, the integration of forge production with food crops significantly reduced soil loss and increased SOM as well as grain yield (Khan et al., 2014; Paul et al., 2020; Drinkwater et al., 2021). Studies of complex paddy rice systems in China that co-produce ducks or fish find multiple benefits including improved nutrient use efficiency and reduced GHG emissions compared to rice monocultures (Nayak et al., 2015).

Case studies: Agroecological management systems and ENM

There are a number of examples where agroecological practices and ENM have been successfully implemented to improve yields and alleviate poverty in smallholder subsistence agriculture (Pretty et al., 2006). Here, we highlight three exemplary farming systems that integrate ENM strategies.

Push-pull polyculture, Sub-Saharan Africa

The groundbreaking push-pull (PP) polyculture system was developed by the International Center for Insect Physiology and Ecology (*icipe*) in western Kenya and uses plant biodiversity to solve the complex, interrelated constraints that limit maize yields in the region (Khan et al., 2008a, 2014). Push-pull polyculture is an inexpensive win-win technology that improves grain yields, livelihoods and human wellbeing while restoring SOM reserves and agroecosystem resilience (Khan et al., 2014; Diiro et al., 2021; Drinkwater et al., 2021). Originally developed to deter lepidopteran pests that damage cereal crops in the region, 20 years of research aimed at meeting the needs of smallholder farmers have yielded an integrated system that delivers a wide range of ecosystem services.

Development of the PP system started with screening hundreds of species to find plants that could either repel key herbivores (push) or serve as trap plants (pull). The resulting PP system consists of *Desmodium* sp. (push) intercropped with maize or sorghum in fields surrounded by trap crop borders (pull). Volatiles released by desmodium repel stemborers and other lepidopterans while the trap crop border simultaneously attracts them out of the field preventing damage to grain crops (Khan et al., 2014). The diversified plant community also attracts natural enemies adding another prevention mechanism to reduce herbivores (Khan et al., 2000).

Push-Pull polycultures provide important belowground ecosystem services. By a stroke of luck, desmodium root exudates induce abortive germination of Striga (*Striga hermonthica*), an endemic parasitic weed which can reduce maize yields by as much as 80%. *Desmodium* intercrops eliminate striga from infested fields (Khan et al., 2000; Hamilton et al., 2012) and, despite shading from maize, *Desmodium* grows vigorously and fixes N, promoting SOM accrual and increasing the capacity of soils to supply N and P (Kifuko-Koech et al., 2012; Drinkwater et al., 2021). Push-pull intercropping leads to substantial increases in N_{org} and plant available P. Gains in N_{org} are divided between MaOM and oPOM pools with oPOM N accounting for >60% of N_{org} accrual (Drinkwater et al., 2021).

A diverse assortment of farmer-centered strategies has been employed to support adoption of PP polycultures. In the context of intensive livestock systems, which creates a demand for high quality forage, adoption has occurred on over 250,000 farms across E. Africa, in part because PP delivers yield and economic benefits within a short timeframe (Khan et al., 2014; Murage et al., 2015). The comprehensive suite of ecosystem services increases maize yields by two- to three-fold compared to maize grown under the typical farmer practices (Khan et al., 2008a, 2014; Midega et al., 2015). Moreover, both Desmodium and border plantings provide high-quality fodder enabling farmers to venture into dairy cattle and goat keeping (Khan et al., 2008b). Lastly, while establishing PP polycultures requires initial investments of seeds and labor, once established labor requirements are modest and income increases, enabling investments in child education and household goods (Diiro et al., 2021).

Parkland agroforestry, West Africa

Parkland agroforestry is an indigenous land use system developed by farmers which allows them to grow annual crops in combination with useful trees and shrubs which are scattered among cultivated fields at varying densities (Boffa, 1999; Masters, 2021). In addition to cereals, farmers draw on a rich legacy of ethnobotanical knowledge to selectively retain native trees within fields and farmland that provide a range of medicinal, cultural, and livelihood functions. For example, Masters (2021) found that parklands systems of four cultures occupying the Aswa River catchment of northern Uganda included 88 indigenous edible plants used as sources of leafy vegetables, roots and tubers, fruits, oils, and seeds.

These systems are most common in arid and semi-arid climates where trees grow as sparse, mixed stands within rainfed staple crop and intercropped fields, frequently in or near riverine areas to tap into deep water sources and support leafing out of trees in the off season. The potential for tree-crop moisture competition is mediated through farmer management that uses intensive pruning and/or burning of lower limbs in tree species. Another common practice involves "reverse phenology" trees such as *Faidherbia* trees that leaf out during the off season when crops have been harvested (Ndoli et al., 2017). This is often (but not always) associated with higher crop yields and improved nutrient efficiency compared with other tree-crop combinations (Ndoli et al., 2017).

Participatory research in Gambia has shown the multifunctional nature of the parkland system, including a variety of ecosystem services valued by farmers (Stoate and Jarju, 2008). The trees generally increase SOM, and N and P availability which can be as much as two-fold higher in cultivated land near tree canopies, compared to non-tree areas. Biological N fixation is an important process supported by inclusion of leguminous trees, which is common in Parkland systems. Acacia and Sesbania species produce biomass N in excess of 150 kg N ha^{-1}, with the exception of very sandy sites where growth is more limited (Chikowo et al., 2006). In this Zimbabwe study, legume leaf mulches increased N supply and maize yields while limiting nitrous oxide emissions. A southern Malawi trial showed accumulation of 12–15% soil C_{org} and POM-N over a decade in a maize-*Gliricidia sepium* agroforestry system (Beedy et al., 2010).

Integration of F_i with organic nutrient sources and the effect of trees on nutrient acquisition and nutrient use efficiency have been the subject of recent research in parkland agroforestry (Diallo et al., 2021). Judicious doses of external nutrients integrated with agroforestry balances nutrient supply and demand resulting in improved nutrient efficiency, as shown in millet (above) and maize fields. On-farm studies of N and P fertilizer use efficiency in *Faidherbia* parklands in Ethiopia and Rwanda suggest that improved nutrient use efficiency is one mechanism contributing to improved grain yields (Sida et al., 2020). In this study, four fertility treatments (0 fertilizer, +N, +P, +N&P at 30 kg ha^{-1} P, 64 kg ha^{-1} N) were compared in open fields and under *Faidherbia* canopies. In general, both crop yields and nutrient use efficiency were greater under tree canopies compared to open fields (Sida et al., 2020).

Parkland agroforestry is an example of a traditional, farmer-developed system which is adapted to local environmental conditions and has been improved by ENM practices that build SOM and improve production and nutrient use efficiency.

Doubled up legumes

Smallholder farmers have limited access to land, labor, and large animals. Thus, plants grown strictly for cover and green manure purposes are rarely feasible to adopt. This can lead to resource degradation, as soil is left bare and residues are minimal in simplified cropping systems with reliance on short growth duration, annual crops. On-farm research has shown that while intercropping systems have yield and nutrition benefits, diversification with annual crops is rarely sufficient to ameliorate soil fertility or restore SOM (Yusuf et al., 2009; Snapp et al., 2010; Nezomba et al., 2015).

One way out of this dilemma is diversification with semi-perennial and indeterminant growth habit crops. Such plant types deliver ENM services while fitting into farming system constraints of small parcels of land. Examples include shrubs such as pigeonpea and spreading forms of cowpea, soybean, and groundnut. These require modest levels of investment in terms of seed, and they can be grown as intercrops and boundary plantings, to be compatible with staple food crops (Bezner-Kerr et al., 2007; Snapp et al., 2019). Growth types are often viney or tall, and produce grain to sell or consume, as well as providing ENM benefits through copious vegetation and deep root systems. Soil organic matter is stabilized through aggregate formation, which protects against physical and biologically mediate degradation processes (Six et al., 2006; Garland et al., 2018); thus it is promising to see evidence of soil aggregation associated with pigeonpea root systems (Spaccini et al., 2004; Garland et al., 2018). Biochemical diversity of aboveground litter is provided through mixed planting of two legumes, which supports ENM function through conserving topsoil, and providing a moist, nutrient rich environment for biological activity, along with enhanced macro pores in some cases (da Silva et al., 2022).

ENM requires attention to enhancing rhizosphere diversity for microbial function, for example, biological N fixation, N mineralization and mobilizing sparingly soluble P. Legumes are universally acknowledged to be an important plant family in such diversification efforts, yet they are often grown at very low intensity within farming systems. Grain legumes are generally sown at low population densities and over limited areas (Mhango et al., 2013), highlighting the need for expanding the legume varieties available, improving agronomy and developing market opportunities. Species such as pigeonpea, groundnut and lupin, have phosphorus-releasing traits such as specialized root exudates and microbial-assisted solubilization, which could be screened to provide improved options for ENM (Ae and Shen, 2002; Tomasi et al., 2008; Garland et al., 2018).

The doubled-up legume system is designed to enhance the presence of legumes, combining tall statured pigeonpea with short-statured groundnut varieties. The species are phenologically complementary, where the rapid early growth of the latter is not suppressed by the former, with its slow initial growth (Snapp et al., 2013). Both species enhance organic pools of soil N and P, although evidence of accrual of total carbon is variable (Witcomb, 2021). Other variations include pigeonpea-soybean and pigeonpea-cowpea doubled-up legumes, grown in rotation with maize (Kalasa et al., 2018). A recent review of innovative sustainable agriculture practices in Africa highlighted this technology as enhancing quality and quantity of grain yield while contributing to integrated nutrient management (Kuyah et al., 2021).

Pathways to implementation of ENM

Agricultural systems are complex, nested social-ecological systems and farm management reflects the surrounding environmental and social context (Liu et al., 2007; Houser and Stuart, 2020). The current system of markets and government policies co-evolved with the dominant input driven, yield focused paradigm and is therefore at odds with agroecological management systems (Deguine et al., 2021). Many recommendations for changes to remove barriers have been proposed with limited success (Bettles et al., 2021; Calo et al., 2021; Vermunt et al., 2022).

Under agroecological practices, including ENM, short-term yield outcomes can vary, and sometimes yields are initially reduced (Ponisio et al., 2015). However, over the long-term, agroecological management will contribute to achieving the UN Sustainable Development Goals (SDGs) by delivering win-win outcomes for farmers and the broader society. ENM promotes diversification at multiple scales, an essential strategy for achieving Sustainable Development Goal #2 (SDG2), which aims to eliminate hunger and malnutrition. Meta-analytical studies find that compared to conventional management regimes, farm-scale diversification increases yields and profitability, improves yield stability and food security, and reduces risk (Himmelstein et al., 2017; Rosa-Schleich et al., 2019; Bezner-Kerr et al., 2021). Furthermore, a recent analysis of FAO data found that cash crop diversification at the national level increases temporal stability of the total national harvest, demonstrating that simply increasing food crop diversity provides a broad societal benefit (Renard and Tilman, 2019).

We consider three aspects of ENM that present challenges to broad adoption of ENM within the existing socio-economic context. First, ENM delivers ecosystem services beyond crop yield; these outcomes receive less support for scientific research and are not incentivized for farmers. Second, some ENM benefits, such as the restoration of the SOM pools, are incompatible with the short timeframe of market and policy incentives which are not equipped to deal with time lags extending beyond a single growing season. Lastly, ENM involves systems approaches to management of SOM dynamics and feedbacks and requires new knowledge and options, such as ENM recommendations and plants with ENM-facilitating traits. Here we discuss essential changes that will advance agricultural diversification and ENM implementation.

Infrastructure to support agricultural diversification

The current socio-ecological matrix can be shifted to implement new, diversification-friendly policies and programs to promote ENM though pathways involving both governmental and non-state actors. In the short-term, modifications to existing policies could fundamentally shift the landscape to favor diversification and ENM. For example, existing fertilizer subsides and other narrow programs could be expanded to promote farmer access to inputs needed to implement diversification and ENM [e.g., seeds and seedlings for planting multiple-purpose and soil-improving species, and livestock; (Khan et al., 2014)]. Subsidies and credit access to reduce risk such as short-term reductions in crop yields would remove one prevalent barrier to ENM implementation. Market failures can also be countered by promoting farmer access to price and market information for a wide range of products beyond commodity crops. Diversification-friendly government policies are needed, including microfinance institutions and policies directed at farmers who want to implement ENM and entrepreneurs who are interested in establishing new enterprises to supply plant materials needed for diversification. Supporting formation of farmer associations for greater market power can also help diversification (Bettles et al., 2021). These actions could provide immediate benefits for smallholder communities.

More fundamental changes to the government policies that shape agricultural development and market forces will require longer timeframes (Calo et al., 2021). One important ENM enabling policy involves the development of markets and funding mechanisms to reward farmers for provision of ecosystem services. This has proven to be controversial and challenging to implement (Kosoy and Corbera, 2010; Kolinjivadi et al., 2015). The difficulty in quantifying ecosystem services such as reduced GHG emissions, SOC sequestration or improved water quality is a major barrier to monetizing ecosystem services beyond yields per hectare. To circumvent the need to monitor actual outcomes at the farm or field scale, policy efforts could target proven management systems and practices using the large body of research linking management to these desirable outcomes. For example, direct payments for agricultural diversification, is one way to incentivize ENM and related management systems that promote ecosystem services (Renard and Tilman, 2019; Tamburini et al., 2020). While the multidimensional benefits of diversification are well-documented, criteria for specific management systems that meet policy goals need to be developed to ensure that diversification schemes are suited for specific environmental and social contexts (Bettles et al., 2021). For example, diversification of cash crops is sufficient for progress with goals related to reduced risk of crop failure and yield stabilization (Renard and Tilman, 2019). However, to promote SOM accrual and deliver a broader suite of ecosystem services that will sustainably improve food security and human wellbeing requires a broader approach to diversification that considers the full range of ecological actors and their ecosystem functions including companion plants that do not have a cash value *per se* as well as integration of plant and animal production (Figure 5).

Expand research portfolio to meet production and sustainability goals

Massive public investments in fertilizer subsidies and a narrow range of crop varieties has come at the expense of investments in knowledge-based ecological management (Ariga et al., 2019). Research priorities follow this lead and concentrate on F_i management with the goal of maximizing yields per hectare, while paying limited attention to the multilayered priorities of farmers and the biological processes governing nutrient cycling in agroecosystems. For example, in a review of more than 200 sustainable intensification studies on smallholder farms, >70% used yield as the primary metric to evaluate technology performance (Reich et al., 2021) and a meta-analysis of N management publications found that only 12% of the data points were from studies of N_{org} sources (Yan et al., 2020).

Several modest course corrections to research will start the process of realigning research to advance agroecological technologies and ENM that are both effective and compatible with smallholder farming systems. On-farm research is now a normative strategy and improved engagement of farmers is essential for meeting the UN Sustainable Development Goals. Farmers possess both experience-based and experimental knowledge of their farming systems, and this perspective adds to scientific knowledge systems and increases the likelihood of successful agroecological cropping system redesigns (Doré et al., 2011). Above all, farmer engagement ensures that performance assessments include farmer indicators and household priorities including yield oriented metrics that are useful to farmers. Yield can be contextualized by expanding yield metrics to reflect farmer priorities such as yield output relative to limited resources such as labor, purchased inputs or water used in irrigation (Avendano-Reyes et al., 2020; Diiro et al., 2021). Research is also needed to address socio-economic barriers to implementing ENM practices, including labor access and land tenure (Calo et al., 2021).

In conjunction with farmer input, better understanding of soil ecological processes and management effects on these processes will reduce the trial and error of cropping systems development and promote development of new agroecological management systems that will improve food security, resilience, and sustainability for smallholder communities across the globe. Research geared toward optimizing management to meet the five ENM guiding principles is urgently needed, such as a better understanding of SOM cycling, plant-microbiome interactions, and organic-nutrient replenishment pathways governing oPOM and MAOM reserves. In particular, management of soil N supply through replenishing SOM reserves deserves more research, as does extension messaging around this approach. Synchrony of N supply, as well as managing fresh residues, partially decomposed and N_{org} pools are all areas critical to ENM.

In the short-term, focusing this research on soil biogeochemical cycling in successful diversification/ENM systems such as those highlighted in the case studies would be a good starting point. To support and improve ENM, research on soil food webs, and delineation of trophic interactions along the lines of the new multichannel model recently proposed is needed (Potapov, 2022). In addition, considering the prevalence of highly weathered acidic soils in regions dominated by smallholder systems, research targeting plant-mycorrhizal associations that can enhance P_i access and facilitate the movement of P_i into P_{org} pools should be a priority (Gianinazzi et al., 2010; Koskey et al., 2021).

Crop breeding programs can advance ENM by intensifying plant selection on several fronts to expand plant traits compatible with ENM regimes. There has been a loss of traits that allow plants to maintain yields under non-saturating nutrient conditions and plant selection approaches may have led to disruption of plant-microbial mutualisms (Perez-Jaramillo et al., 2016; Jaiswal et al., 2020; Isaac et al., 2021). Over the near-term improvements could be made in breeding for ENM. This includes profiling existing cultivars and companion species for their belowground traits to jump-start breeding efforts. Substantive differences in belowground traits occur across existing cultivars and characterizing the impact of species/cultivars on key SOM pools will identify cultivars that have greater potential to perform well under ENM and enable more targeted EMN strategies. For example, rhizosphere priming of SOM varied from 8 to 18 μg C g^{-1} soil across maize lines (Gowda et al., 2021) and stabilization of root-derived C varied by 70% among barley cultivars (Mwafulirwa et al., 2021). Inclusion of neglected crop species, landraces and cultivars that may have superior adaptations to local conditions can expand belowground traits and genetic resources available for breeding programs.

Over the longer-term, investments are needed in the development of cultivars that possess a wider range of nutrient acquisition strategies, and that benefit from plant-microbial partnerships. Cultivars of important food crops need to be bred for improved performance in diversification schemes ranging from cultivar mixtures to polycultures and agroforestry systems (Bourke et al., 2021; Wuest et al., 2021). Development of improved cover crops and other companion species is clearly needed, with traits that maximize belowground ecosystem services such as oPOM and MAOM accrual. Expanding the companion species toolbox will broadly support diversification beyond ENM implementation and provide multiple benefits including improved food security and resilience (Tamburini et al., 2020; Bezner-Kerr et al., 2021). Bringing farmers to the table to expand the knowledge base and engage in participatory breeding programs has proven to be beneficial for developing genotypes that are better adapted to farmers' needs (Alves et al., 2018). In the long-term, development of perennial and semi-perennial staple crops would provide tremendous advantages over annuals in terms of soil restoration and sustainability (Crews et al., 2016).

Investments in education and dissemination

Lack of ecological literacy among agronomists, extensionists and farmers is another barrier to agroecological management systems such as ENM and marked expansion of education on agroecology is needed at all levels (Deguine et al., 2021). Universities, public educational institutions, and government extension could all be important sources of agroecology training if this were the focus of education efforts. In wealthy nations, universities are offering graduate programs in agroecology and this trend needs to be promoted more broadly in developing nations (Eksvard et al., 2014). ENM can be enhanced by extension education that promotes understanding of SOM functions, nutrient cycling processes and biodiversity-ecosystem function concepts. A well-rounded ecological knowledge base is informed by formal education but includes informal learning and indigenous knowledge (Occelli et al., 2021). For example, farmers understand that legumes increase soil N fertility, but they often lack knowledge of key factors that govern N fixation rates as reflected by the high rates of N fertilizers some farmers apply to legume-grain intercrops (Drinkwater et al., 2021). For ENM to be adaptable to local conditions, peer knowledge is important, and can be facilitated through the support of networks for farmer to farmer exchange and curricula that build on local knowledge (Bezner-Kerr et al., 2019). Farmer-farmer learning, participatory extension and farmer field schools are all effective strategies for fostering farmer agency and agroecological management (Doré et al., 2011).

Another key area of investment is tools and training in on-farm problem solving for adaptive management, an essential element of ENM and all agroecological management systems (Lin, 2011). Farmers develop their own systems for evaluating performance and troubleshooting, and these strategies can be supplemented with technologies that can be used in the field (Falkowski and Drinkwater, 2020). Newly developed handheld sensors and digital tools that measure soil C_{org} levels are one example; feedback on soil C_{org} accrual is valuable to farmers who practice ENM and for implementing payments for C sequestration (Tieszen et al., 2004). For instance, in Malawi, inexpensive handheld sensors enabled extension educators to visit with farmers and provide reliable information on real-time soil C_{org} status and crop N response (Ewing et al., 2021).

Conclusion

Under the dominant agricultural production regime, farmers use fertilizers and other agrochemicals to maximize yields and to compensate for loss of the ecosystem services once provided by species diversity. This choice of crop yield as the primary performance indicator is particularly untenable given the limited resources and widespread abject poverty of rural communities in the developing world. In fact, the promotion of resource intensive agricultural technologies combined with the constraints imposed by poverty and food insecurity have fueled pervasive soil degradation. Farmers are caught in a vicious cycle where declining soil function requires intensification and increases the need for purchased inputs to produce crops, which only reinforces the trend of soil degradation—in essence, a fertilizer treadmill.

Reversing this downward spiral in the face of a changing climate coupled with unfettered intensification and widespread ecosystem degradation requires a change in strategy. Agroecological approaches and the use of agricultural diversification to restore ecological integrity provide the most promising pathway for advancing sustainable poverty alleviation and food security in regions where malnutrition and hunger are endemic. Ecological nutrient management falls within the portfolio of ecologically based management and offers a comprehensive approach to soil fertility. It recouples elemental cycles, promotes conservation pathways and gradually rebuilds SOM for resilience. ENM rests on a solid foundation of ecosystem and biogeochemical scientific understanding, and despite the many barriers imposed by current agricultural policies, successful ENM systems are being used by smallholder farmers with promising results. Likewise, there is progress in some development organizations in recognizing the value of agroecological management systems including ENM; however, policy changes that promote an enabling environment are essential for implementation of ENM and sustainable solutions to malnutrition and food insecurity.

Author contributions

LD and SS jointly developed the structure and content of the review and jointly conceptualized the pathways section. LD conceptualized and drafted the ENM guidelines, ecosystem processes and ecological nutrient management sections, the push-pull case study, figures, and tables. SS drafted the pathways section and the parkland and doubled up legumes case studies. Both authors contributed to drafting the conclusions and editing the entire manuscript.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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Trade-offs in organic nutrient management strategies across mixed vegetable farms in Southwest British Columbia

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Balancing economic and environmental objectives can present trade-offs for organic farmers maximizing crop yields while maintaining core principles of ecology and health. A primary challenge for achieving this balance is nitrogen (N) and phosphorus (P) management. Meeting crop N requirements with compost can build soil carbon (C) and soil health but often over-applies P and increases soil P and associated environmental risks. Alternatively, high-N organic fertilizers can provide N without surplus P but can be expensive and lack C inputs that composts supply. We evaluated these potential trade-offs in 2-year field trials on 20 mixed vegetable farms across three regions of Southwest British Columbia, Canada, capturing a range of climatic-edaphic conditions and organic amendments. Three nutrient management strategies were evaluated: *High Compost*: compost applied to meet crop N removal, *Low Compost + N*: compost applied to meet crop P removal plus an organic fertilizer to meet crop N removal, and *Typical*: varying combinations of composts and/or organic fertilizers ("typical" nutrient application on the farm). Nutrient strategies were evaluated in terms of yield, input costs, and soil properties [permanganate oxidizable C (labile C responsive to soil management), and post-season available N and P]. Soil P was 21% higher with *High Compost* than *Low Compost + N*. In one region characterized by inexpensive but nutrient-rich composts and soils high in P, input costs were lowest with *Typical,* but in the second year, *High Compost* outperformed *Typical* in crop yield. Principal component analysis showed a divergence in post-season NO_3^- between nutrient strategies in relation to compost and soil properties: *High Compost* using high-N composts increased post-season NO_3^- (0–30 cm), whereas relative yields in *High Compost* tended to be higher on farms with lower soil C and lower C:N composts, while yields with *Typical* were higher under opposite conditions but associated with higher post-season NO_3^-. Combining input types (e.g., *Low Compost + N*) can meet environmental objectives in reducing surplus soil P without short-term yield

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or cost trade-offs compared to *High Compost*. However, maintaining soil C needs to be investigated to achieve effective ecological nutrient management in organic vegetable production with improved nutrient balances.

KEYWORDS

organic agriculture, nitrogen, phosphorus, manure, compost, ecological nutrient cycling, organic fertilizer, organic amendments

Introduction

Organic agriculture aims to sustain healthy people, soils, and ecosystems through a reliance on ecological processes, biological cycles, and biodiversity (Gomiero et al., 2011). With this set of ambitious social and environmental goals, researchers and policymakers have proposed organic farming systems as a way to achieve sustainable agricultural development (Seufert, 2012). This also calls for enhanced production of regionally-grown, nutritious food that supports the livelihoods of small- and medium-scale farmers. Balancing environmental and economic objectives, however, is a particular challenge for organic farmers as they strive to maximize crop yields while maintaining core organic principles of ecologically based management. While organic agriculture can be beneficial for local economies (Marasteanu and Jaenicke, 2019), nutrient management, especially soil nitrogen (N) availability (Berry et al., 2002; Seufert et al., 2012), is a key challenge to organic farming systems contributing to agricultural productivity goals, and (de Ponti et al., 2012); organic farmers rank nutrient management as a top research priority (Jerkins and Ory, 2016).

Organic amendments (e.g., composts, manures, specialty fertilizers) and cover crops are used both for in-season nutrient supply and to build soil organic matter (SOM) to provide long-term soil fertility (Gomiero et al., 2011). However, these inputs have a range of biochemical properties, and unknown or uncertain nutrient content, that make it difficult to predict nutrient supply and match crop nutrient demand (Gale et al., 2006; Maltais-Landry et al., 2016). Vegetable crops—the focus of this study—require relatively high amounts of soil mineral N [ammonium (NH_4^+) and nitrate (NO_3^-)] during the growing season, but excess amounts post-harvest can be lost to the surrounding environment, especially through NO_3^- leaching in regions with high rainfall (Maltais-Landry et al., 2019). For any nutrient management approach, a careful assessment of production, economic, and environmental outcomes that accounts for variation in local conditions is required to reduce potential trade-offs and ensure sustainability goals are met.

Balancing nutrient budgets is a central goal of ecological nutrient management (Drinkwater and Snapp, 2007) but is challenging when composts are the primary nutrient source. Applying these types of amendments to meet crop N demand is common on organic farms, but the high P to plant-available N (PAN) ratio in these amendments relative to crop requirements builds up soil P over time (Watson et al., 2002; Nelson and Janke, 2007; Maltais-Landry et al., 2016; Carr et al., 2019). This problem is exacerbated by low first-year N availability in these amendments, including immobilization of N from the soil mineral pool (i.e., −10% to +54% of total N; Gale et al., 2006), in contrast to greater first-year P availability (i.e., +70% to +100% of total P; Nelson and Janke, 2007). As an alternative, or in combination with composts and manures, farmers can use biological N fixation from leguminous cover crops and/or apply specialty organic fertilizers to meet crop N demands while adding little to no P.

High-N but low-P specialty organic fertilizers (e.g., feather meal, blood meal, alfalfa meal/pellets, fish meal), can help balance N and P budgets (Maltais-Landry et al., 2016; Sullivan and Andrews, 2017), but these inputs can be relatively expensive, especially by comparison in regions with intensive livestock industries where manures are abundant (Spargo et al., 2016; Reid et al., 2019; Svanbäck et al., 2019). Reducing compost applications to not exceed crop P requirements provides much less C than when applied to meet crop N requirements (Eghball, 2002; Maltais-Landry et al., 2019), and at typical rates of application, specialty organic fertilizers are limited sources of C compared to composts (White et al., 2020). The impact of changing nutrient management strategies on soil C is important to assess, but difficult to measure with common indicators such as SOM and total soil organic C (SOC) given their slow rate of change (Gregorich et al., 1994; Bünemann et al., 2018). More responsive soil health indicators such as permanganate oxidizable C (POXC) and polysaccharides are likely to provide better insight into the effects of different amendment combinations on soil health (Bünemann et al., 2018).

With varied topographies, climates, and soil types, the province of British Columbia (BC) provides unique conditions for diverse agricultural crops and types of production systems. One of the main agricultural regions in BC is the lower Fraser Valley, where 29.8% of all farms and 26.4% of certified organic farms in the province are located (Government of British Columbia, 2017). Rising land prices coupled with emerging markets outside of urban centers are opening opportunities for agricultural production in other areas of BC such as Vancouver Island and Pemberton Valley. Those two regions have fewer animal livestock operations than the lower Fraser Valley, and thus less access to manure-based composts. High precipitation in the non-growing season across all regions makes NO_3^- leaching of particular concern. With unique soil types, climatic conditions, and types of available organic amendments among these three agricultural regions, nutrient strategy performance among the regions would most likely be different.

This study evaluated ecological nutrient management practices on working mixed vegetable farms in three agricultural regions of southwest BC (the lower Fraser Valley, Pemberton Valley, and Vancouver Island). This study is aimed at overcoming the constraints of research station studies, which can have limited applicability outside of the climate, soil, and management conditions at one or two study sites (Vanlauwe et al., 2019). Our multi-site study introduces greater heterogeneity in field conditions (i.e., background variability) to better understand how treatments perform under real, but varied, agronomic and economic conditions on working farms (Coe et al., 2019). We compared three treatments that represent common but contrasting nutrient management approaches: ***High Compost***: Compost applied at a rate to target crop N removal, ***Low Compost + N***: Compost applied at a rate to target crop P removal plus an organic fertilizer (feather meal) at a rate to meet crop N removal, and ***Typical***: The nutrient application that the farmer would typically use for the specific crop (varying combinations of organic fertilizers, composts, and manures, or no amendments applied). The specific objectives of this study were to evaluate the effect of these three nutrient strategies on farms across the three regions on crop yield, input costs, and selected soil properties [POXC, and post-season available N (NO_3^- and NH_4^+) and available P], and identify the farm site edaphic, environmental, and input quality factors that affect nutrient strategy outcomes, particularly any trade-offs among them.

Materials and methods

Field trials were established in the spring of 2018 on vegetable farms that rely on organic amendments in three regions of southwest BC: the lower Fraser Valley, Pemberton Valley, and Vancouver Island; see Supplementary Figure 1 for a map of farm site locations in the three regions. A total of 20 different farms participated over the 2-year study period, with 19 farms in the first year and 18 in the second year. Sixteen out of the 20 farms were certified organic, while four were using organic nutrient management practices, but were not certified organic. The farms in this study sell directly to customers (e.g., farmers' markets or similar programs). As part of this direct marketing strategy, these farms also grow a large diversity of crops (30–50 different vegetable, herb, or fruit types each year), with the exception of one farm which specializes in growing fewer crops for wholesale markets (e.g., corn, beans, peas, potatoes, barley). All farms in this study are primarily mixed vegetable farms and use intensive tillage. Additional characteristics of the three regions are summarized in Table 1, and additional farm characteristics are provided in Supplementary Table 1.

Experimental design

At each of the farm sites, the following three nutrient management strategies were evaluated:

- ***High Compost***: Compost was applied to meet crop N removal (the amount of N exported from the field with crop harvest);
- ***Low Compost + N***: Compost was applied to meet crop P removal (the amount of P exported from the field with crop harvest) and a feather meal fertilizer was applied to meet crop N removal;
- ***Typical***: Varying combinations of organic fertilizers, composts, and manures, or in some cases, no amendments, were applied. This was the "business as usual" nutrient application that each farmer uses for their farm and was different for each farm. The amendments used for *Typical* were determined by each farmer for the *Typical* plot on their farm and we simply quantified these for this study.

Each nutrient strategy treatment was established in one plot per farm site, so each farm site in each year had a total of three plots. Within each farm site and year, all plots were managed the same and only differed by the nutrient strategy applied. Plot size depended on the size of the farm but averaged 29.3 m^2 and ranged from 6.3 to 100.0 m^2. Overall, the research plots at 11 farm sites received the same nutrient management strategy for 2 years, and at 23 farm sites for 1 year.

Crops grown in the research plots in 2018 included beet (*Beta vulgaris* L. subsp. *Vulgaris*), broccoli (*Brassica oleracea* L. var. *botrytis* L.), carrot (*Daucus carota* L. subsp. *sativus*), cauliflower (*Brassica oleracea* L. var. *botrytis* L.), potato (*Solanum tuberosum* L.), and pickling cucumber (*Cucumus sativus* L.), and in 2019 included cabbage (*Brassica oleracea* L. var. *capitata*), carrot, beet, onion (*Allium cepa* L. var. *cepa*), and potato. The distribution of these crops across the farms' research plots is shown in Supplementary Table 1.

Amendment rate calculations

Amendments were applied at rates to target crop-specific N and P removal. Estimates of crop N and P removal in harvests were determined from target (or expected) yields chosen by each farmer for their crop. Nutrient concentrations from local data

TABLE 1 Characteristics of the three study regions in Southwest British Columbia, Canada.

Characteristic	Region		
	Lower Fraser Valley	Pemberton Valley	Vancouver Island
Climate[1]	Moderate maritime	Continental	Moderate maritime
Soil drainage[2]	Poorly drained	Poorly to imperfectly drained	Poorly to imperfectly drained
Soil texture[2]	Fine texture	Fine texture	Fine to medium texture
Soil parent material[2]	Fluvial	Fluvial	Marine deposits
Soil types[2]	Rego Humic Gleysol, Humic Luvic Gleysol, and Orthic Humic Gleysol	Rego Gleysol and Gleyed Regosol	Brunisol and Gleysol subgroups[3]
Soil P	High	Low	Low
Livestock density	High	Low	Low

1 Government of Canada (2019).
2 Government of British Columbia (2018).
3 The Vancouver Island region spans a larger geographic area than the other two regions, and therefore has the most diverse soil types.

were used, but if not available then crop-specific recommended nutrient application rates from best-available sources were used as target nutrient application rates instead. Target nutrient application rates used in this study are summarized by general crop groups in Table 2 and data sources and nutrient application rates are listed in Supplementary Table 1.

Composts were unique to each farm and were either currently being used by the farmer or we sourced them from regionally-available options. Composts therefore varied widely in their composition due to varied feedstocks and sources and compost C:N ratios ranged from 9.3 to 39.4 (unpublished data). Composts were applied on various spring and summer dates to match when the farm would be planting; see Supplementary Table 2 for the mean and median amendment application rates, application dates, and associated C, N, and P application rates by nutrient strategy and region. All composts and fertilizers were weighed and broadcast by hand, then incorporated into the soil either by hand by us or by the farmer with tractor-mounted equipment.

For *High Compost*, compost was applied at a rate where the estimated rate of crop removal N was matched with the estimated in-season PAN from the compost. For *Low Compost + N*, both compost and feather meal were used: compost was applied at a rate where the estimated rate of crop removal P was matched with total P from the compost, and feather meal was applied at a rate to supply PAN to match the difference between PAN applied with the compost and the estimated crop removal N.

Estimated compost PAN was calculated as 15% of the compost organic N plus the compost inorganic N (NH_4^+ and NO_3^-). A 15% mineralization rate was used based on the literature and a conservative approach to ensure adequate N availability from a variety of composts and manures (Gale et al., 2006). These calculations were made using the following equation:

$$\textbf{Equation 1: } \boldsymbol{PAN = \left(Total\ N - Inorganic\ N\right) * 0.15 + Inorganic\ N}$$

Two different feather meal products were used in *Low Compost + N* because of regional availability. A feather meal with reported 11% N (11-0-0, Natures Intent, Pacific Calcium Inc., Tonasket, WA, USA) was used on all farms in the lower Fraser Valley and Pemberton Valley and a feather meal with reported 13% N (13-0-0, Gaia Green, Grand Forks, BC, Canada) was used for all farms on Vancouver Island. For both feather meal products, calculations were based on "guaranteed" total N concentration reported by the manufacturer (on the bag label), and 100% of this N was assumed to become PAN during the growing season, (i.e., 100% mineralization). The C:N ratios of the Gaia Green and Nature's Intent feather meals were 4.2 and 5.3, respectively. Adjustments for moisture content were made in calculations for composts but not for the dried feather meal fertilizer products.

Amendments were weighed and applied by hand to *High Compost* and *Low Compost + N* plots using shovels, a 5-gallon bucket, and a field scale. Amendment application rates in *Typical* were quantified in two ways. If amendments were spread by hand, we weighed and applied them by hand based on instructions from the farmer. Alternatively, if a tractor-mounted compost spreader was used, then we used a tarp and 1 m × 1 m quadrat to measure the application rate. Briefly, we first covered the two research plots (*High Compost* and *Low Compost + N*) with a heavy-duty poly tarp held in place with ground staples. The farmer then drove over the tarped area while spreading manure at their typical rate with a tractor-mounted compost spreader (applying amendment directly onto the *Typical* plot as they went). Next, 51 m^2 subsamples of compost were collected from the tarp and the weight of

TABLE 2 Estimated nitrogen (N) and phosphorus (P) crop removal rates (kg ha^{-1}) based on pre-season estimated yields, averaged across major crop categories.

Crop	*n*	N			P		
		Mean ± SD	Min.	Max.	Mean ± SD	Min.	Max.
Potato	10	73 ± 27	21	116	12 ± 5	4	20
Carrot	7	66 ± 22	40	97	12 ± 4	7	18
Beet	7	128 ± 50	51	215	18 ± 7	8	30
Brassicas*	4	138 ± 55	59	181	35 ± 27	11	73

Values shown are number in each category (*n*), mean ± standard deviation (SD), minimum (min.) and maximum (max) values.
*Brassicas include broccoli, cabbage, cauliflower, and kohlrabi.

amendment collected from each subsample was recorded. The subsamples were averaged to represent what was spread on the *Typical* plot (kg amendment m^{-2}).

All farms in this study use cover crops as part of their overall management, but only five farms (two in 2018 and three in 2019) had winter cover crops in the research plots before the growing seasons in which our research took place. Cover crops were observed to be uniform across the three plots at the five farm sites with cover crops; one farm site had fall rye (*Secale cereale* L.), one farm site had fall rye, hairy vetch (*Vicia villosa* Roth), and winter peas (*Pisum sativum* L.), and the other three had fall rye, hairy vetch, and crimson clover (*Trifolium incarnatum* L.). Given the challenge of coordinating sampling with farmers, and that so few farms had cover crops, N inputs from cover crops were not included in the estimate of N supply from the nutrient strategies.

Soil and compost sampling and analyses

Compost analyses

Compost samples were taken directly from compost piles at each farm during initial farm visits on various dates in the spring of both years of the study. Five subsamples of roughly 0.5 L volume and from 0.5 m depth into the pile were collected from different locations on the pile and mixed thoroughly to make a composite sample. Compost was analyzed at the BC Ministry of Environment and Climate Change Strategy Analytical Laboratory (MOE), Victoria, BC, Canada for NH_4^+ and NO_3^-, total C, N, P, and K, pH, EC, and water content.

Within 72 h of sample collection, NH_4^+ and NO_3^- were measured using a 2 *M* potassium chloride (KCl) extraction (Maynard et al., 2008) and analyzed colorimetrically using an A2 Analyzer (Astoria-Pacific, Clackamas, USA) (Weatherburn, 1967; Doane and Horwáth, 2003). Total P and K of composts were determined by microwave-assisted acid digestion using an ultraWave microwave (Milestone, Sorisole, Italy; Karam, 2008) then element concentrations were determined by ICP-OES on a Prodigy Spectrometer (Teledyne Leeman Labs, Mason, OH, USA). Total C and N were measured by combustion on a Flash 2000 Elemental Analyzer (Thermo Fischer Scientific Inc., Waltham, MA, USA; Thermo Fisher, 2010). Electrical conductivity was measured using a 1:4 compost to water ratio with 5 g of compost shaken with deionized water (Hendershot et al., 2008a) and conductivity was read on a conductivity meter and small volume flow-through cell. Varying compost to water ratios were used to measure pH, depending on the compost. First, deionized water was added to 5 g of compost and stirred. After resting for 30 min, the suspension was stirred again, and pH was measured with a pH meter (Hendershot et al., 2008b).

Compost bulk density was measured on farm sites using a 5-gallon bucket (Washington State University, 2020). First, a scale was tared to the weight of an empty 5-gallon bucket, then the bucket was filled 1/3 full of compost taken from a hole dug in the compost pile (not from the dry outer layer). Next, the bucket was dropped ten times from a roughly 0.3 m height onto a hard surface. The bucket was then filled to 2/3 full of compost, dropped ten times again, filled to full, and dropped ten times again. Finally, the bucket was filled to full again and the weight was taken, and the compost bulk density was calculated by dividing by the volume of the bucket. This was repeated three times and the average was used.

Soil analyses

Depending on conditions, soil samples were collected using either a soil auger (5.5 cm inner diameter) or probe (1.9 cm inner diameter). Ten to fifteen subsamples were taken from each plot when using a probe, or five subsamples when using an auger to account for differences in sampling volume. Soil samples were taken three times at all farms in 2018 (pre-season, mid-season, and post-season) and two times for all farms in 2019 (mid-season and post-season), except for at the three new farm sites in 2019 that were not included in the first year of the study, where pre-season samples were also collected in 2019. Pre-season soil samples were analyzed at the same laboratory (MOE) as compost samples and mid- and post-season soil samples were analyzed in our lab.

Pre-season soil samples were analyzed for a variety of properties and were collected at two depths (0–15 and 15–30 cm) prior to applying amendments. Within 72 h of collection, samples were analyzed for NH_4^+ and NO_3^- using a 2 *M* potassium chloride (KCl) extraction using the same methods as described previously for composts. The remaining sample was dried (35°C), ground, and sieved to <2 mm particle size prior to all other analyses. Percent sand, silt, and clay were determined using the hydrometer sedimentation method with water maintained at 25°C and particles were dispersed using Calgon detergent prior to analysis (Kroetsch and Wang, 2008). Total C and N were measured by combustion on a Flash 2000 Elemental Analyzer (Thermo Fischer Scientific Inc., Waltham, MA, USA; Thermo Fisher, 2010) and inorganic C was measured on a Primacs SNC-100 TN/TC Analyzer (Skalar, Breda, the Netherlands; Skalar Analytical, 2019). Available P and potassium were measured from 2.5 g of soil with 25 mL of Mehlich-3 extractant (Ziadi and Sen Tran, 2008). After filtration the element concentrations were determined by ICP-OES on a Prodigy Spectrometer (Teledyne Leeman Labs, Mason, OH, USA). Electrical conductivity was measured using a 1:2 soil water ratio with 10 g of soil shaken with deionized water in a 50 mL centrifuge tube for 1 min then centrifuged for 10 min (Hendershot et al., 2008a). For pH a 1:1 soil water ratio with 10 g of soil was used (Hendershot et al., 2008b).

Mid-season soil samples were analyzed for POXC. Samples were collected in July both years at one depth (0–15 cm) from within crop rows. Soil samples were air-dried and sieved to 2 mm, then 2.5 g of soil was combined with 18.0 mL of distilled water and 2.0 mL of 0.2 *M* potassium permanganate ($KMnO_4$) solution adjusted to pH 7.2 (Weil et al., 2003) and analyzed on a 96-well plate on a TECAN Spark® spectrophotometer at 550 nm (TECAN Group Ltd., Mannedorf, Switzerland). For one farm site with high SOM [SOC ~10%; POXC > 2,500 mg kg^{-1})], 1 g (instead of 2.5 g) of soil was used to avoid full consumption of MnO_4^- in the reaction (Wade et al., 2020; Liptzin et al., 2022).

Post-season soil samples were analyzed for available N and P and were collected at two depths (0–15 and 15–30 cm) after crops had been harvested (between September 25 and October 16). Samples were collected prior to the latest date for a valid post-harvest nitrate test (PHNT) according to provincial guidelines (Government of British Columbia, 2019), which account for soil texture and local precipitation. Samples from both depths were analyzed for NH_4^+ and NO_3^- by extracting 2.5 g of field-moist soils with 25 mL of 2 *M* potassium chloride (KCl) (Maynard et al., 2008) and were measured colorimetrically (Weatherburn, 1967; Doane and Horwáth, 2003) using a spectrophotometer (Bio-Rad iMark, Hercules, CA, USA). Samples from only the surface depth (0–15 cm) were air-dried and sieved and were analyzed for Kelowna-extractable P (van Lierop, 1988) by extracting 2.5 g of air-dried soils with 25 mL of a solution of 0.015 *M* ammonium fluoride (NH_4F) and 0.25 *M* acetic acid (CH_3COOH) and were determined on a Varian 725-ES ICP-OES (Agilent Technologies, Mulgrave, Victoria, Australia). To determine soil water content, the weight of a field-moist soil sample was recorded before and after oven drying for 48 h at 105°C.

Crop yield sampling

The number of crop biomass subsamples taken per plot was equal to or >30% of the total crop area in a given plot, minus the area used as buffers on the plot perimeter (between two to ten subsamples, depending on plot size). Subsamples were averaged and recorded as the weight of crop biomass per one bed meter (kg m^{-1}). Harvest dates, plot sizes, and number of subsamples taken per plot are shown in Supplementary Table 1. Plot buffer widths varied between 0.5 and 2.5 m, depending on farm management and type of tillage equipment used. A stratified sampling method was used to choose subsample locations in each plot. Subsamples were taken by placing a 1 m × 1 m quadrat on top of a crop bed, then all marketable crop biomass (e.g., potato tubers but not tops, cabbage heads, beets with tops) between the two ends of the quadrat were harvested and weights were recorded.

Estimating input costs

Input cost data was collected from each farm and includes both the amount paid for the amendment as well as associated shipping or transportation costs. Input costs are reported in Canadian (CAD) dollars per hectare ($ ha^{-1}), as a function of the input costs and their rate of application, extrapolated to 1 hectare. Most farmers within the study have their off-farm amendments delivered to the farm and therefore provided us with shipping costs as part of this calculation. For farms that pick up amendments locally, the farmer's time and vehicle mileage were valued at $20 h^{-1} and $0.59 km^{-1}, respectively, and were applied to an estimate of round-trip time and mileage, which were provided by the farmer. Any inputs that did not include the two nutrients being studied, N or P (e.g., lime, micronutrients, etc.), were not included in the total cost because they were applied to all three plots and not examined in this study. In the case where the farm was unable to report/estimate shipping costs, the cost was estimated based on nearby farms or estimated mileage costs to the nearest available retailer.

Statistical analyses

We performed all analyses in R (R Core Team, 2019). For various reasons (e.g., farms harvested before our sampling, crop failure, unreported input costs), not every farm site has a complete data set for each year (i.e., all five outcomes). Overall, 63% of farm sites have complete datasets, and sample sizes are reported for each analysis.

We used linear mixed-effects (LME) models to account for the impact of the farm-specific, variable background characteristics on the mean response of the measured outcomes (e.g., yield, POXC, etc.) for each farm site (Crawley, 2013; Krzywinski and Altman, 2014; Webster and Lark, 2018), and to account for autocorrelation of repeated measures where the same plots were sampled from in both years (Krzywinski et al., 2014). We considered each year within one farm as a nested random effect in the model. We performed all analyses with the *lme* function in the *nlme* package version 3.1-143 (Pinheiro et al., 2019) using the maximum likelihood (ML) method for model comparisons and the restricted maximum likelihood (REML) method for reporting final model output. As the primary explanatory variable of interest, we included nutrient management strategy as a categorical fixed effect with three levels (*High Compost*, *Low Compost + N*, and *Typical*). We included year (2018 and 2019), region (lower Fraser Valley, Pemberton Valley, and Vancouver Island), and all interactions as fixed effects to investigate if the impact of nutrient strategy on the dependent variables was different between years or regions (i.e., to consider interactions). We tested assumptions of normality and homogeneity of variance using the Shapiro-Wilk test and Bartlett test, respectively, and we transformed data if needed to meet assumptions.

We performed stepwise elimination of terms in the LME models to identify the most parsimonious model based on AIC (Crawley, 2013) and marginal and conditional R^2 values (Nakagawa and Schielzeth, 2013); we report output from performing ANOVA for each of the selected LME models. When there were significant interactions between the fixed effect of nutrient strategy and region and/or year, we ran the model separately to assess nutrient strategy within a year and/or region. When the main effect of nutrient strategy was significant in the LME model ANOVA, a post-hoc (Tukey method) test was used to determine significant differences between factor levels using the *emmeans* function (Lenth, 2019). We determined differences to be significant for p-values < 0.05, and marginally significant for p-values < 0.10. ANOVA F and p-values are reported in Supplementary Tables 3–9. When LME models were run with nutrient strategy and cover crops (presence or absence) as fixed effects, we found that the impact of nutrient strategy on measured outcomes did not vary by the presence or absence of cover crops (nutrient strategy × cover crop interaction was not significant) and, thus, cover crops were not further considered in our analysis.

We used principal component analysis (PCA) using the *FactoMineR* package (Husson et al., 2020) to assess how the nutrient strategy outcomes (yield and post-season NO_3^-) covary with each other, farm site pre-season soil properties [soil C and available soil P (0–15 cm)], and farm-specific compost properties (compost total N and P, and compost C:N). We focused on yield and post-season NO_3^- as outcomes in the PCA as they represent a direct trade-off between productivity and environmental impacts. We plotted each outcome as data relativized at each farm site by dividing each observation within a farm site by the farm site average. This allows the outcomes in the PCA to vary by the impact of nutrient strategy rather than between-farm variation. We did not plot pre-season soil or compost variables that are auto-correlated (e.g., soil total N and total organic C). We transformed non-normally distributed data to satisfy conditions of normality for the PCA.

Results

Soil properties: POXC and post-season available N and P

Differences in post-season available N were observed among nutrient strategies in the upper depth (0–15 cm), but not in the lower depth (15–30 cm). Specifically, while post-season NO_3^- (0–15 cm) did not differ among nutrient strategies across region and years (Figure 1A), a region-specific response was observed (nutrient strategy × region interaction, $p = 0.010$). When analyzed by region, the main effect of nutrient strategy was marginally significant in the lower Fraser Valley and Pemberton Valley (Supplementary Table 7), with trends of greater post-season NO_3^- (0–15 cm) with *High Compost* and *Typical* than *Low Compost + N* in the lower Fraser Valley, and opposite trends in Pemberton Valley (Figure 1B), although none of these differences were significant in the post-hoc test. Across regions and years, *Typical* and *High Compost* had higher post-season NH_4^+ (0–15 cm) than *Low Compost + N* (Figure 2A). However, the impact of nutrient strategy on post-season NH_4^+ varied among the regions (nutrient strategy × region interaction, $p = 0.003$), and when analyzed by region, the main effect of nutrient strategy was significant in the lower Fraser Valley and on Vancouver Island, but not in the Pemberton Valley (Figure 2B). On Vancouver Island, post-season NH_4^+ (0–15 cm) was lower in *Low Compost + N* than *Typical* (Figure 2B). In the lower Fraser Valley, there was a trend of less NH_4^+ (0–15 cm) with *Low Compost + N* than *High Compost* (Tukey contrast, $p = 0.052$).

The overall trend in post-season available P matched the order of average total P applied with each nutrient strategy, of *High Compost* > *Typical* > *Low Compost + N* (Supplementary Table 2). However, only *High Compost* and

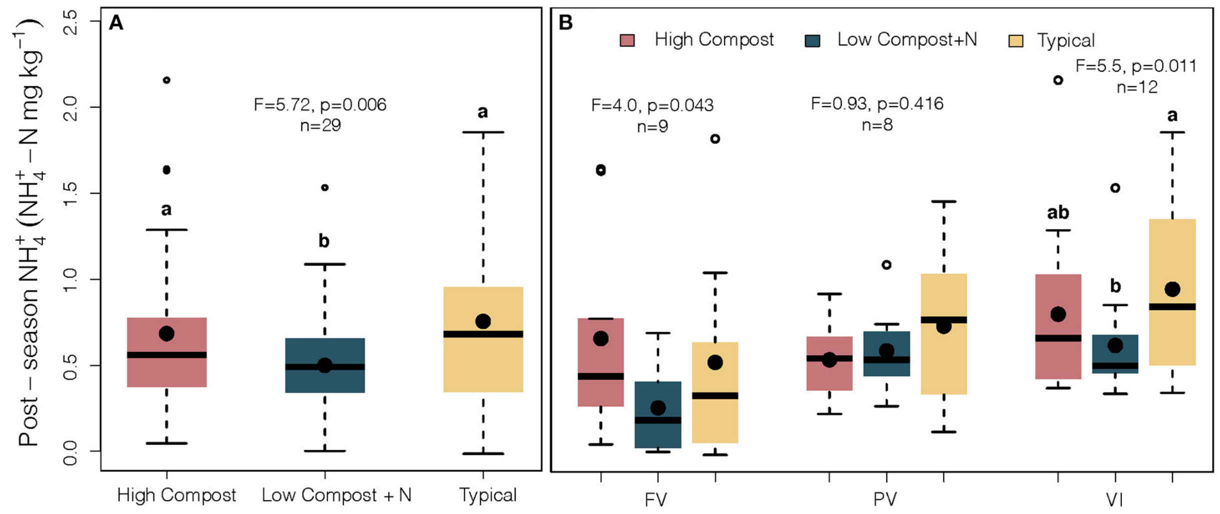

FIGURE 1
Boxplots of post-season NO_3^--N (mg kg^{-1}) (0–15 cm). **(A)** By nutrient management strategy, across regions and years, and **(B)** by nutrient management strategy within three vegetable production regions of British Columbia [lower Fraser Valley (FV), Pemberton Valley (PV), and Vancouver Island (VI)] over years. ANOVA *F* and *p*-value refer to main effect of nutrient strategy. Boxplots with different letters represent significant differences among nutrient strategies using Tukey's post-hoc test at $p < 0.05$. The center line indicates the median, means are shown as black dots, sample size is indicated by *n*, and the Tukey-style whiskers extend to a maximum of 1.5 the interquartile range.

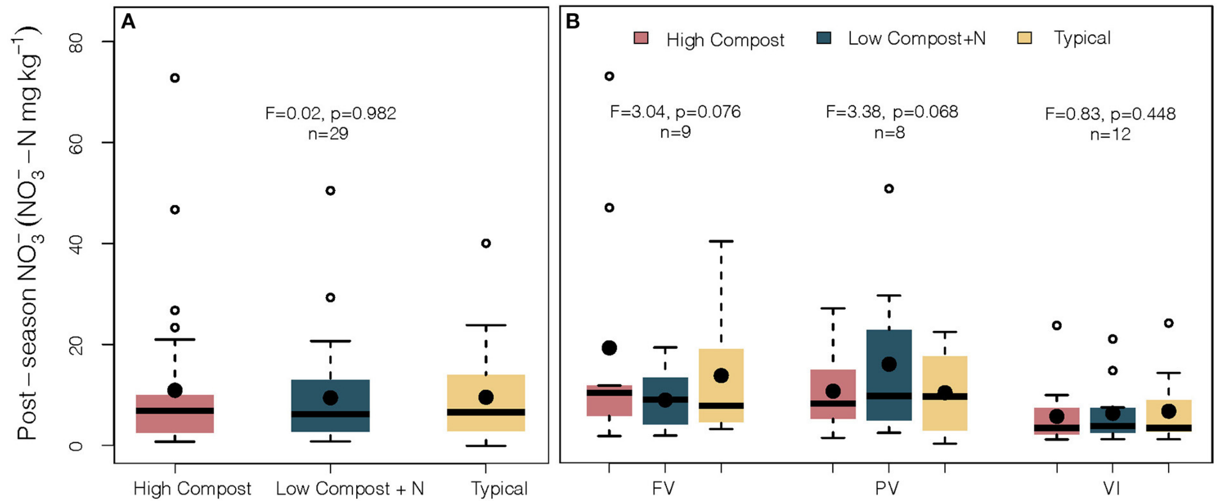

FIGURE 2
Boxplot of post-season NH_4^+-N (mg kg^{-1}) (0–15 cm). **(A)** By nutrient management strategy, across regions and years, and **(B)** by nutrient management strategy within three vegetable production regions of British Columbia [lower Fraser Valley (FV), Pemberton Valley (PV), and Vancouver Island (VI)] over years. ANOVA *F* and *p*-value refer to main effect of nutrient strategy. Boxplots with different letters represent significant differences among nutrient strategies using Tukey's post-hoc test at $p < 0.05$. The center line indicates the median, means are shown as black dots, sample size is indicated by *n*, and the Tukey-style whiskers extend to a maximum of 1.5 the interquartile range.

Low Compost + N were significantly different (Figure 3). Permanganate oxidizable C varied widely among farms, and ranged from 248 mg kg soil^{-1} on a farm transitioning from conventional to organic management to 3,042 mg kg soil^{-1} on an urban farm with high C inputs. Mean POXC across all treatments, regions, and years was 1,102 mg kg soil^{-1}; POXC was not different among nutrient management strategies.

Crop yield

Overall, crop yields did not show consistent differences among nutrient strategies, but a region- and year-specific response was observed (nutrient strategy × region × year interaction; $p = 0.044$). In the lower Fraser Valley ($p = 0.031$), yields were higher with *High*

Compost than *Typical* in 2019 ($p = 0.033$) but not in 2018 (nutrient strategy × year interaction, $p < 0.001$; Figure 4).

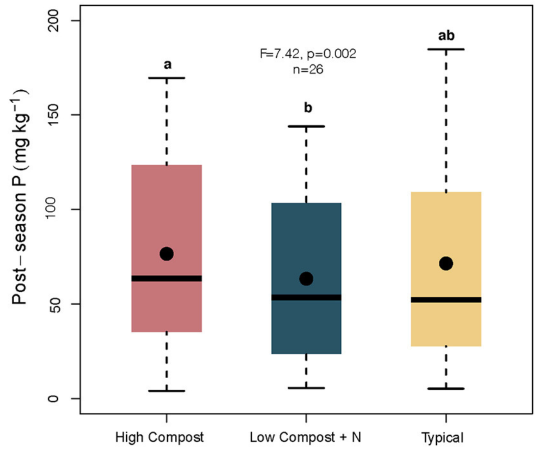

FIGURE 3
Boxplot of post-season available P (mg kg^{-1}) by nutrient strategy, across years and three vegetable production regions of British Columbia. ANOVA *F* and *p*-values refer to main effect of nutrient strategy. Boxplots with different letters represent significant differences among treatments using Tukey's post-hoc test at $p < 0.05$. The center line indicates the median, means are shown as black dots, sample size is indicated by *n*, and the Tukey-style whiskers extend to a maximum of 1.5 the interquartile range.

Input costs

The cost of amendments as determined within the scope of this study was highly variable, especially for *Typical*, which ranged from \$0 with no nutrient application, to \$34,977 ha^{-1} with an expensive compost. Overall, the mean cost of inputs (per nutrient strategy) was \$4,959 ha^{-1}. Although we did not find consistent differences in input costs among the nutrient strategies, a region-specific response was found (nutrient strategy × region interaction, $p = 0.002$). In the lower Fraser Valley, *Typical* had lower input costs than both *High Compost* and *Low Compost + N* (Figure 5).

Principal component analysis

Covariation in nutrient strategy outcomes and baseline farm site soil and compost properties were well described by the first and second principal component axes (~50% of total covariation), with PC1 and PC2 explaining 28 and 19% of total variation, respectively (Figure 6). Nutrient strategy outcomes differentiated on the first two PCA dimensions, and region had a significant effect on observed covariation described by both PC1 ($p = 0.010$) and PC2 ($p = 0.047$). Pre-season soil P, compost total N and P contents, compost C:N, and relative post-season NO_3^- in *Low Compost + N* and *High Compost* plots were significantly correlated with PC1

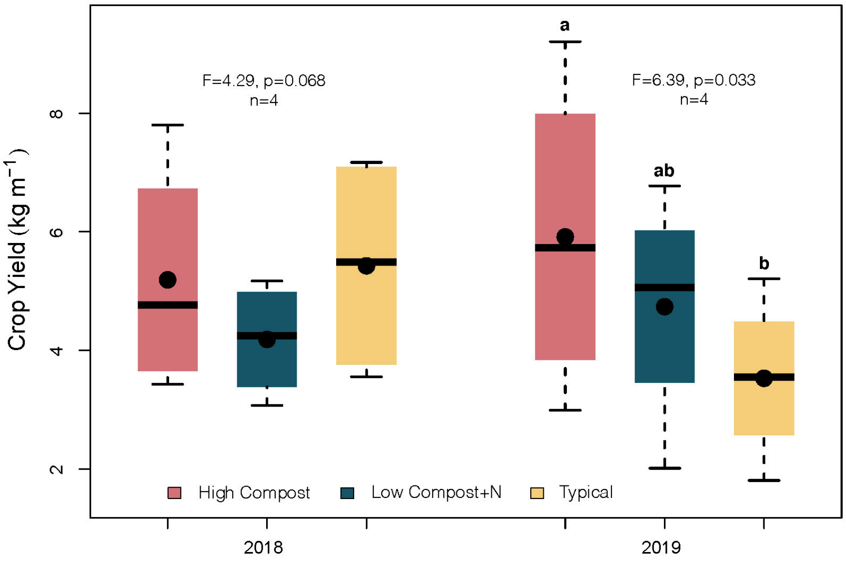

FIGURE 4
Boxplot of yield (kg m^{-1}) in the lower Fraser Valley of British Columbia by nutrient management strategies within each year of the study. ANOVA *F* and *p*-values refer to main effect of nutrient strategy within year. Boxplots with different letters represent significant differences among treatments using Tukey's post-hoc test at $p < 0.05$. The center line indicates the median, means are shown as black dots, sample size is indicated by *n*, and the Tukey-style whiskers extend to a maximum of 1.5 the interquartile range.

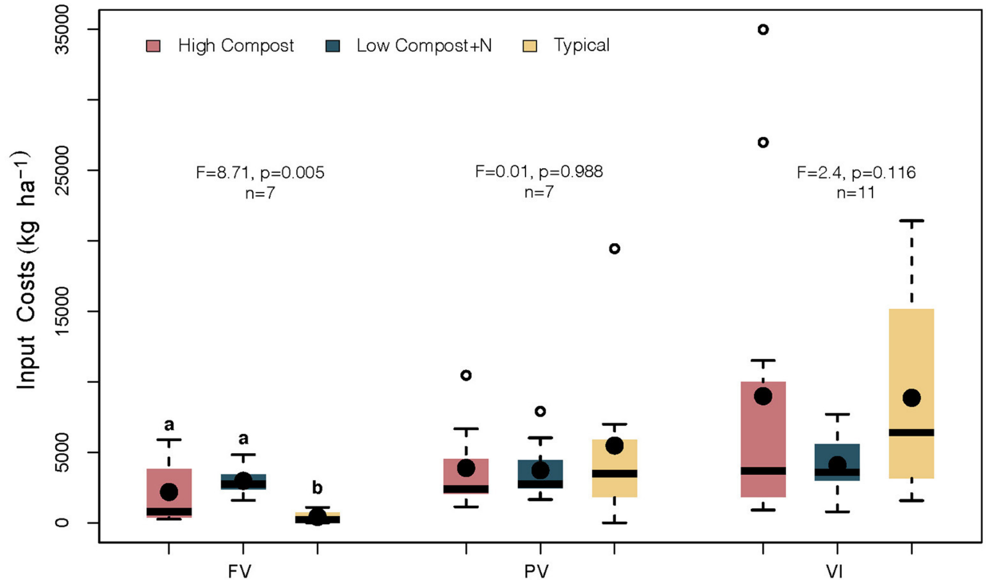

FIGURE 5
Boxplot of input costs (\$ ha^{-1}) by nutrient management strategy across years within three vegetable production regions of British Columbia [lower Fraser Valley (FV), Pemberton Valley (PV), and Vancouver Island (VI)]. ANOVA *F* and *p*-values refer to main effect of nutrient strategy within each region. Boxplots with different letters represent significant differences between nutrient strategies using Tukey's post-hoc test at $p < 0.05$. The center line indicates the median, means are shown as black dots, sample size is indicated by *n*, and the Tukey-style whiskers extend to a maximum of 1.5 the interquartile range.

(Supplementary Table 10). On this first axis, farms with higher pre-season soil P that were using composts with higher N and P contents, coordinated with higher relative post-season NO_3^- in *High Compost* plots characterized by higher PC1 scores, which tended to be on farms in the lower Fraser Valley. In contrast, relative post-season NO_3^- with *Low Compost + N* coordinated negatively with PC1 and characterized farms with lower pre-season soil P and that used composts with higher C:N; farms on Vancouver Island tended to have lower PC1 axis scores. The second axis described variation in soil C and compost C:N, along with relative post-season NO_3^- in *Low Compost + N* and *Typical*, and relative crop yields in *High Compost* and *Typical* (Supplementary Table 10). On PC2, relative yields in *High Compost* tended to be higher on farm sites that had low soil C but also used composts with lower C:N. Relative yields in *Typical* were higher under the opposite conditions but with a concomitant environmental trade-off of relatively higher post-season NO_3^-. This nutrient strategy-specific relationship between yield and post-season NO_3^- was also found when yield was used as a predictor variable of post-season NO_3^- in the linear mixed effects model to explicitly evaluate for a key production-environment trade-off (nutrient strategy × yield interaction, $p = 0.002$). Increasing yields were significantly associated with increasing post-season NO_3^- with *Typical* nutrient strategy, and the opposite was observed with *High Compost* (Supplementary Tables 11, 12).

Discussion

Effects of nutrient strategies on measured outcomes

Identifying nutrient management strategies based on organic amendments that can optimize yields, balance nutrient budgets, and supply C to maintain SOM are fundamental to meeting both economic and environmental goals. However, meeting crop nutrient requirements on mixed vegetable farms can be particularly challenging. Organic systems tend to be N limited, and organic farms are more likely to maximize yields in crop types with greater N use efficiency, such as legumes and perennials (Seufert et al., 2012). Our results of the short-term impacts of three organic nutrient strategies place *Low Compost + N* as being most likely to meet both environmental and productivity goals of organic vegetable production.

Variable impacts on soil properties

A major difference among nutrient strategies was post-season soil P, which was 21% higher with *High Compost* than *Low Compost + N*. On average, *High Compost* provided over 8× more P than the amount of crop P removal (harvest; Supplementary Table 2). Other studies have also found that large compost applications at ∼5× crop P removal (similar to *High*

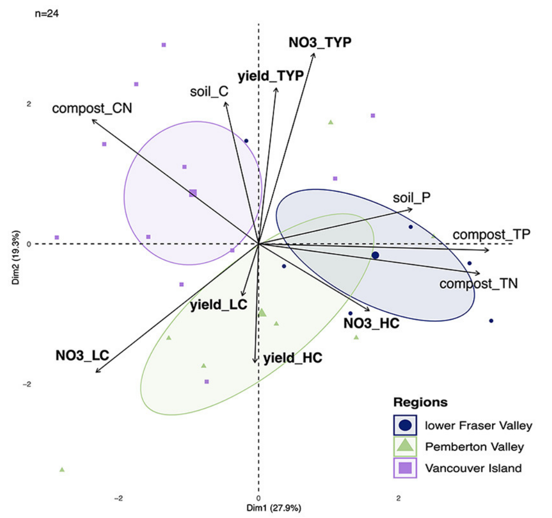

FIGURE 6
Principal Component Analysis (PCA) biplot of relative post-season NO_3^- (0–30 cm) and relative crop yield following each nutrient management strategy (*Typical* (TYP), *Low Compost + N* (LC), and *High Compost* (HC)). Outcomes by nutrient strategy are plotted with pre-season compost and soil properties including compost total N (compost_TN), compost total P (compost_TP), compost C to N ratio (compost_CN), and pre-season soil total organic C (soil_C), pre-season soil P (soil_P). Pre-season soil samples are averages for the three research plots at each farm. Variables are grouped by each of three vegetable production regions of British Columbia (lower Fraser Valley, Pemberton Valley, and Vancouver Island). The large data points are mean values for each region and the ellipses are 95% confidence intervals. The sample size for each measured outcome within each nutrient strategy is indicated by *n*.

Compost in this study) and high manure applications at 4× crop P removal, increased soil P in comparison to smaller compost applications (Evanylo et al., 2008; Maltais-Landry et al., 2019). In contrast, Mkhabela and Warman (2005) did not find differences in available P (Mehlich-3 extractable) among corn and potatoe plots receiving 1 or 2 years of compost at 1×, 2×, and 3× crop P removal (much lower than *High Compost* in this study) in Wisconsin. There was often large quantities of P applied with *Typical* amendment applications (Supplementary Table 2), which would likely increase soil P on many of the farms in our study if these practices are ongoing. Therefore, switching from *Typical* to a *Low Compost +N* strategy would avoid environmental risks of excess soil P.

We did not observe differences in post-season available NO_3^- among nutrient strategies which suggests similar nutrient availability and uptake in crops (with similar yields), regardless of amendment type and/or combination. Post-season NO_3^- leaching has been strongly linked to the quantity of N applied (Drinkwater and Snapp, 2007), and in our study, mean total N applied to *High Compost, Typical,* and *Low Compost + N* was 474, 372, and 153 kg N ha^{-1}, respectively. Thus, the very high total N inputs in *High Compost* could mineralize more than expected and/or asynchronously with crop N uptake, thus increasing environmental risk. However, low levels of post-season NO_3^- in our study (mean = 9.1 mg NO_3^--N kg^{-1} soil at 0–30 cm depth) suggests these nutrient strategies were not systematically over-applying N; although there were differences in post-season NH_4^+ among the nutrient strategies, values were also generally low. We did, however, find post-season NO_3^- levels in several plots to be greater than the provincial threshold for environmental protection (25 mg NO_3^- kg^{-1} soil (∼ 100 kg NO_3^--N ha^{-1}); Government of British Columbia, 2019); values above this can require follow-up soil testing and nutrient management planning (depending on location and type of farm). There were four plots (two from *High Compost* and one each from *Low Compost + N* and *Typical*) with post-season NO_3^- above this threshold. These make up only 5% of all plots in our study, yet demonstrate that organic agriculture is not inherently without environmental impacts (Tuomisto et al., 2012). Variable soil properties, precipitation, and sampling times between harvest and post-season NO_3^- sampling (0–2 months) across the different farms in our study likely contributes to some inaccuracy in characterizing post-harvest NO_3^- as a site's potential for N leaching. Future work is needed to develop more systematic methodology of assessing post-harvest NO_3^- and linking with potential for N leaching on diverse organic farms.

The large variability we observed in POXC was mainly attributed to the overall management context of the farm and not the nutrient strategies we tested, and is comparable to similar farming systems elsewhere. POXC ranged from 661 to 1,070 mg kg^{-1} (measured on 5 g, 2 mm-sieved soil) and from 154 to 983 mg kg^{-1} (measured on 2.5 g, 2-mm sieved soil) on organic vegetable farms in southwestern Ontario, Canada (Hargreaves et al., 2019) and in New York, USA (Culman et al., 2012; unpublished data cited by Culman et al., 2012), respectively. Despite being regarded as a management-sensitive indicator, POXC did not register the 1 and 2 years of substantially different C inputs among nutrient strategies in our study (see Supplementary Table 2). This potentially reflects the need to perform POXC analysis based on a fixed SOC mass rather than a fixed soil mass (Pulleman et al., 2021) or with an increased number of replicates (Wade et al., 2020) in order to increase the sensitivity, and therefore usefulness, of this indicator.

Economics: Balancing input costs and yields

As expected, yields did not consistently differ by nutrient strategy given they were all designed to meet or exceed crop N and P removal. Similarly, a 3-year study in Virginia, USA found no yield differences in vegetables (pumpkin, bell pepper, and corn) grown using a high compost application (targeting crop N requirements) or a low compost application plus a (conventional) N fertilizer, reportedly due to soil nutrient reserves and adequate nutrient supply from amendments

(Evanylo et al., 2008). The only exception where we found yield differences was in the Fraser Valley in the second year of the study, where yields were greater in *High Compost* than in *Typical*. It is possible that these yield differences were observed in the lower Fraser Valley, but not in the other two regions, because farms in our study in the lower Fraser Valley are more similar to each other (have more similar farm site characteristics, including high soil P and composts with high N and P content; data not shown), whereas farm site characteristics were more varied amongst farms in the other two regions.

Further, yield differences in the lower Fraser Valley could be due to differences in PAN applications between the treatments. In the Fraser Valley in study year two, there was less estimated PAN applied to *Typical* than was applied to *High Compost* on three farms (103 vs. 115, 42 vs. 87, and 0 vs. 46 kg PAN ha^{-1} applied to *Typical* vs. *High Compost*, respectively), whereas on one farm, substantially more PAN was applied to *Typical* than to *High Compost* (530 vs. 97 kg PAN ha^{-1}, applied to *Typical* vs. *High Compost,* respectively). Similarly, Evanylo et al. (2008) found lower corn yields with smaller compost applications (supplying 20% of crop PAN requirements) compared to larger compost or poultry litter applications (supplying 100% of crop PAN requirements); the same study found a positive correlation between soil NO_3^- and corn earleaf N. Additionally, reduced potato yields from over application of N fertilizer was found by Reiter et al. (2012) when comparing four N fertilizer rates (0, 67, 134, 201, and 268 kg N ha^{-1}) in potato production, where the middle rate (134 kg N ha^{-1}) produced the highest yields. This suggests that amendment application rates based on site-specific but simple nutrient budgets can help prevent under- or over-fertilization and optimize yields. Given that crops on organic farms can be N-limited due to issues with timing, rather than total amounts of N mineralized and available to plants (Berry et al., 2003), additional tools and indicators tailored to ecological nutrient management could build on nutrient budgets to further enhance nutrient use efficiency in these systems (Drinkwater and Snapp, 2007; Bowles et al., 2015).

Although we had expected that meeting crop N requirements with specialty organic fertilizers would cost more than with composts or manures, this was not the case, and instead we found a surprising amount of variation in amendment costs both within and across the regions. The widely varied geography of BC plays an important role with input cost differences across island, mountain, and river valley regions that characterize the agricultural landscapes here. Off-farm and out-of-region fertilizers and composts are subject to additional transportation and distribution costs for Vancouver Island or Pemberton Valley farmers who are separated from the concentration of agricultural suppliers in the lower Fraser Valley. Farmers in the lower Fraser Valley are clearly choosing the most economical nutrient strategy, where costs of *Typical* were less than both *High Compost* and *Low Compost + N*. However, yields were greater in *High Compost* vs. *Typical,* which represents a context-specific trade-off in farmers' current nutrient strategies, in terms of input costs and yield gains. Overall, *Low Compost + N* had the least variability among regions, given that it is less dependent on the highly variable cost of compost.

The costs we estimated in this study were much higher than the \$700 ha^{-1} reported for pelletized poultry manure and pig manure for potatoes in Truro, Nova Scotia, Canada (Lynch et al., 2008), although *High Compost* and *Typical* were <\$800 ha^{-1} when using inexpensive poultry manure-based amendments in the lower Fraser Valley. Our estimates were more similar to organic nutrient inputs for vegetable production in California (~\$1,561 and \$2,247 ha^{-1} for broccoli and lettuce, respectively; assuming \$1 USD ~ \$1 CAD in 2011) (Klonsky, 2012). Overall, our observations highlight the range in fertility costs for organic farms in southwest BC, which largely depend on the regional availability of composts, manures, and specialty organic fertilizers.

Covariation of nutrient strategy performance and farm site characteristics

While we did not find overall differences in post-season NO_3^-, and only minor differences in crop yield among nutrient strategies, there was differentiation between these outcomes when analyzed with farm site characteristics in PCA. Our data show a divergence in post-season NO_3^- between *High Compost* and *Low Compost + N* in relation to the nutrient content in composts used and pre-season soil P, highlighting the complex nature of amendment-soil interactions on organic farms. Farm sites using high nutrient composts tended to have high post-season NO_3^- when large quantities of compost were used (*High Compost*). A meta-analysis by Norris and Congreves (2018), also found that C-based amendments high in N (such as poultry manure) increased risk for NO_3^- leaching. In the lower Fraser Valley, Sullivan and Poon (2012) similarly found more than 2× higher post-season NO_3^- in manured vegetable fields compared to fields that did not receive manure.

Differentiation of yields amongst nutrient strategies was unrelated to coordinated variation in initial soil P levels and the N and P content of composts used at an individual farm site. Notably, high yields with *Typical* were associated with high post-season NO_3^-; this relationship was also significant when yield was used as a predictor variable of post-season NO_3^- in the mixed effects model, and follows observations of nutrient saturation reported in intensive annual crop production (Drinkwater and Snapp, 2007). Additionally, these outcomes from *Typical* did not characterize a particular region but did covary with increased soil C and higher compost C:N. This could reflect an over-application of N fertilizers by farmers aiming to avoid N immobilization with high C:N amendments. Indeed other studies have found that N fertilizers increase vegetable yields when farmers rely on composts with high C:N (e.g., Mkhabela and Warman, 2005; Evanylo et al., 2008), although we did not observe this in our study.

Balancing trade-offs of nutrient management strategies

To illustrate trade-offs among nutrient strategies and across regions, outcomes (yield, input costs, POXC, post-season NO_3^-, post-season P) were plotted in radargraphs (*fsmb* package; Nakazawa, 2019) and axis limits were set to the highest value among the three nutrient strategies (Figure 7). There were limited and region-specific trade-offs among nutrient management strategies, whereby improvements in the outcomes of one or more productivity and/or environmental metric co-occurred with detrimental or more negative results in other outcomes. Across regions and years, nutrient strategies did not have significant differences in yields, POXC, post-season NO_3^-, or input costs, but *High Compost* did have higher post-season P than *Low Compost + N*.

There were region-specific differences in nutrient strategy performance in the Fraser Valley, with trade-offs in crop yields, costs, and potential environmental impacts. In this region, input costs with *Typical* were lower than *High Compost* and *Low Compost + N*, but *High Compost* had greater yields than *Typical* in 1 year in this region, but also greater post-season available P than *Low Compost + N*. *High Compost* in this region has a potential trade-off between yield and environmental impacts, yet recommending *Low Compost +N* over *Typical* to reduce potential environmental impacts could increase costs for some farmers.

Implications for farm management

Results of this study underscore the contexts where different organic nutrient management strategies can best perform in achieving sustainable agricultural development, as well as the key challenges that farmers face in doing so. In the lower Fraser Valley, *High Compost* had higher yields than *Typical* but the PCA also suggests that using *High Compost* on farms with high soil P and high-N composts (as found in the Fraser Valley) can increase risk for high post-season NO_3^-. Overall, *Low Compost + N* did not appear to have environmental trade-offs (i.e., high post-season N or P), however, using *Low Compost + N* will require alternative C inputs to maintain SOC. Cover crops could provide C inputs and potentially capture post-season NO_3^- and provide biological N fixation (from legumes), but will incur additional costs and management complexity. Cover crops are challenging for various reasons, including short shoulder seasons, high land prices, increased management complexity, and grazing by overwinter waterfowl in the lower Fraser Valley (Merkens et al., 2012). Combining cover crops with reduced compost applications is an important area for further research.

As environmental costs are not directly paid for by the farmer, but reduced yield and increased input costs are, it is difficult to reason that farmers using composts as affordable sources of C and N (as in the lower Fraser Valley) should change their practices to decrease soil P and post-season available N from a purely (farm-level) economic standpoint. Farms likely need incentives (e.g., economic rewards, technical support) to balance farm N, P, and C budgets using high-N specialty fertilizers and/or more intensive cover crop use and reduced compost applications. At a global level, policymakers are introducing nutrient management regulations, such as the "Code of Practice for Agricultural Environmental Management" in BC (Government of British Columbia, 2020), the "Vermont Pay-For-Phosphorus Program" (State of Vermont, 2021) in the USA, and various approaches in countries surrounding the Baltic Sea in Europe (Svanbäck et al., 2019).

Farms in regions without easy access to inexpensive, high nutrient composts (e.g., Pemberton Valley and Vancouver Island) may have more economic incentive (without policy interventions) to employ lower compost application rates. These farms can combine cover crops, fertilizers, and compost, depending on how their viability, costs, and availability, respectively fluctuate from season to season. Given that the yield differences we found in the lower Fraser Valley could be due to differences in N management, all farms would benefit from basic annual PAN budgeting to avoid excessive N deficits or surpluses in each season. In contrast, P budgets have greater annual flexibility, where farms with low soil P can over-apply P and farms with high soil P can under-apply P in the short term. In the long term, the *Low Compost + N* strategy is favorable because it sets the farm field P balance at zero.

Ecological nutrient management can contribute to achieving Sustainable Development Goals (SDG) 2.3 and 2.4 [particularly as these SDGs are clarified by Gil et al. (2019)], which call for advancing both farm productivity and sustainability. However, our study highlights the importance of assessing management practices with multiple, and often competing, end-results, and the need for region- and farm-specific management decisions that can be flexible to system-specific input and soil properties. This study contributes to the emerging literature aimed at policy-makers who are concerned with improved understandings of the contexts where organic agriculture can best perform in terms of meeting sustainable agricultural development goals (Seufert, 2012; Ramankutty et al., 2019). Efforts to optimize farm- or field-level nutrient budgets and build SOC should additionally consider socio-economic factors governing landscape-scale nutrient flows which influence

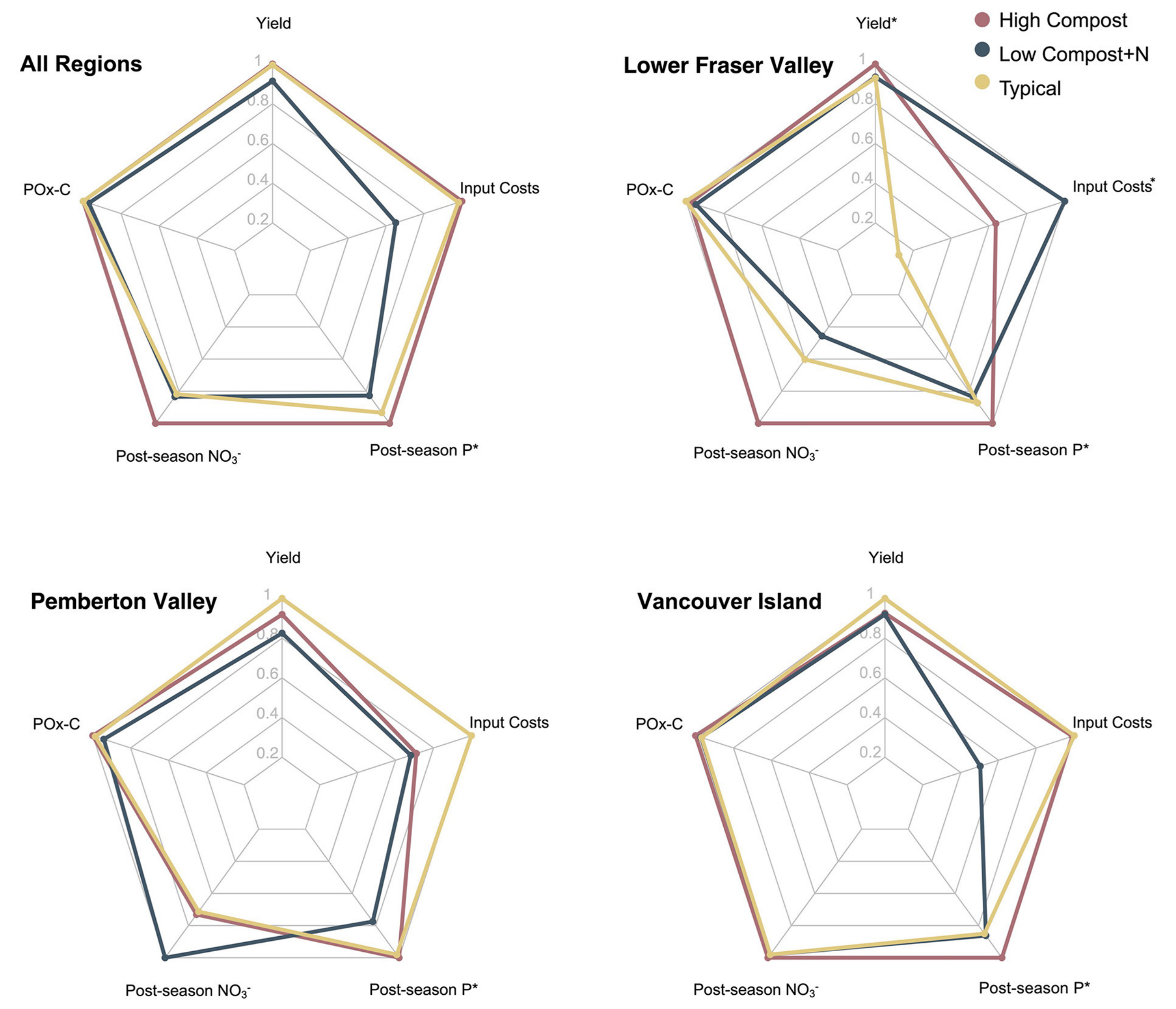

FIGURE 7
Measured outcomes scaled to the maximum value observed among nutrient strategies, expressed as the mean within each nutrient strategy, averaged across all farms (All Regions) and across all farms in each of three vegetable production regions in British Columbia. Measured outcomes include: yield, input costs, post-season available P (0–15 cm), post-season NO$_3^-$ (0–30 cm), and permanganate oxidizable carbon (POXC). Measured outcomes with significant differences at alpha <0.05 between nutrient strategies are indicated with an asterisk (*).

on-farm management practices (e.g., cost and availability of nutrient inputs).

Conclusions

Nutrient management strategies must be evaluated for potential trade-offs that can depend on regional nutrient availability to ensure productivity does not compromise sustainability goals. There were inconsistent trade-offs among the three nutrient strategies compared on 20 working farms across three distinct regions. The typical nutrient management approach used by each of the farmers varied widely, which contributed to challenges in identifying systematic differences between these typical nutrient combinations and our two standardized nutrient strategies. Regardless of regional differences in soils and amendments, post-season P was significantly lower when compost was applied to meet crop P removal instead of crop N removal. Our results show that a nutrient management strategy which combines reduced compost with organic N fertilizer is most likely to meet both environmental and productivity goals. However, long-term research on the impacts to, and strategies to maintain, SOC is required. Given that economics is the key driver for farmer decision making, future research should also include a more substantial economic analysis to thoroughly capture costs and benefits including labor, crop quality, and cover crops.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

AN project lead, conducted the experiment, completed data analysis, and wrote the manuscript. DL project concept, technical guidance on experimental setup and data collection, and manuscript revision. KB technical guidance on data collection, analyses, interpretation, and manuscript revision. MK and JC conceptual guidance and manuscript revision. SS project concept, project design, acquired funding, data interpretation, and manuscript revision. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fsufs.2022.706271/full#supplementary-material

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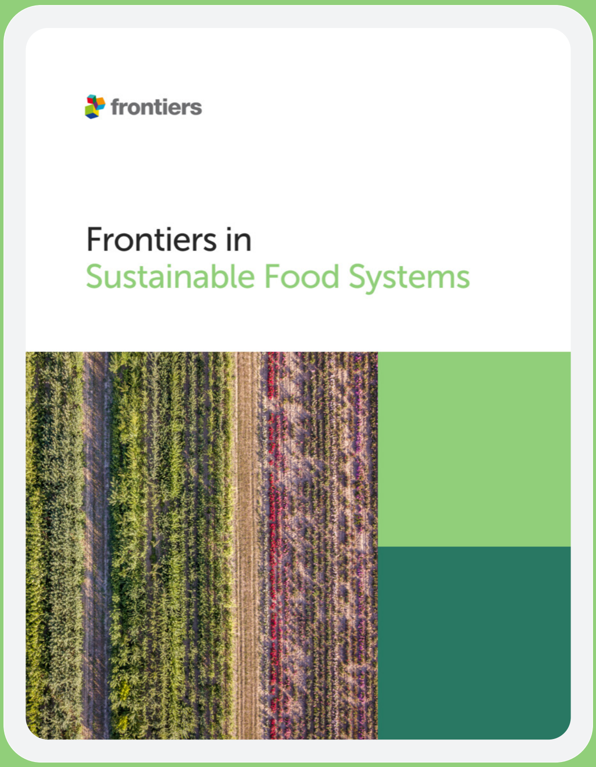

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